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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

UNITED NATIONS ENVIRONMENT PROGRAMME

INDICES FOR MEASURING RESPONSES OF AQUATIC ECOLOGICAL SYSTEMS TO VARIOUS HUMAN INFLUENCES

A report of the ACMRR/IABO Working Party on Ecological
Indices of Stress to Fishery Resources

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, 1976

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PREPARATION OF THIS REPORT

This document was prepared by the ACMRR/IABO Working Party on Ecological Indices of Stress to Fishery Resources as a part of a cooperative project of the United Nations Environment Programme entitled:

Effects of Pollutants on Living Aquatic Resources and Scientific Basis for Monitoring

with the Food and Agriculture Organization of the United Nations as cooperating agency. The working party met twice, under the chairmanship of H.A. Regier, once at FAO headquarters, Rome, Italy 4-11 December 1974 and once at the University of Toronto, Toronto, Canada 30 June-7 July 1975.

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Ecology. Ecosystems. Pollution monitoring. Pollution effects. Information handling. Mathematical models. Fisheries statistics. Fishery management.

PREFACE

Following the 1970 FAO Conference on Marine Pollution, held in Rome, the ACMRR Secretariat proposed a working party on "the application of ecological theory to exploitation and conservation of marine fisheries resources". The working party was to produce a brief, semi-technical review of available broad ecological models and of information applicable to the problem areas in conservation and management of fishery resources, both with respect to exploitation and pollution. It was hoped that this report could provide decision-makers with a broad view of the field, the technical and practical man with a guide to useful advice, and the theoretical ecologist with a stimulus to apply his insights to practical ends.

Further discussions during the meeting of the Joint Working Party on Global Investigation of Pollution in the Marine Environment (GIPME) in San Marco di Castellabate 11-18 October 1971 underscored the need for a "broadly planned ecological approach" to the study of marine pollution problems.

There was broad support given to ACMRR's pollution concerns at the United Nations Conference on the Human Environment held in Stockholm. Subsequently, upon the establishment of the United Nations Environment Programme, a cooperative project of UNEP and FAO was established entitled "Effects of Pollutants on Living Aquatic Resources and Scientific Basis for Monitoring". This project opened the way for examining a number of aspects of aquatic pollution. In its seventh session, ACMRR reviewed the earlier recommendations and agreed to the establishment of three working parties to examine various aspects of the effects of pollution on living aquatic resources. One of these was to be on "ecological indices of stress to fishery resources".

The working party was promptly formed with Professor H.A. Regier, of the University of Toronto, as convener and chairman. The group met twice, first in Rome, 4-11 December 1974, and then in Toronto, 30 June-7 July.

In the two sessions possible with the funds available, the activities of the Working Party could not extend beyond a feasibility study for a programme to mobilize technical competence, available theory and accessible data. It is this study which is reported here.

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1. OBJECTIVES

1.1 Terms of reference

Our objectives in this study have been specified as follows (see section 5.2 of reference ACMRR, 1974):

"The Committee endorsed the following terms of reference for this group:

For purposes of measuring, surveying and monitoring the impact of pollution, nutrient enrichment, modification of water flow, and similar technological stresses on living aquatic resources:

(i) to bring together for critical review such indices as have already been proposed;

(ii) to propose guidelines for the selection and/or formulation of well-balanced sets of indices;

(iii) to propose new indices for further research and testing;

(iv) to evaluate the usefulness of such indices as measured, say, by the relative cost of the practical information that they provide; and

(v) to develop guidelines for pilot studies and research projects to be incorporated into on-going activities of FAO and other bodies as well as relevant programmes such as GIPME.

The Committee agreed that the ecological indices to be considered should relate to the following levels of organization in marine and freshwater systems: population, community, ecosystem, with special emphasis on community indices. Bio-assay and toxicity tests, aiming at the organism and population levels should be excluded here as should also the complex functions which might derive from extended and intensive analysis of functional dynamic models. Emphasis should be placed on sets of indices which together are adequate to discriminate among the effects of various natural factors, technological stresses, and fisheries exploitation."

1.2 Comments on terms of reference

Following its first meeting in Rome our working party reviewed the terms of reference to determine in what manner and to what extent we might satisfy our duties.

(i) The first term (see above) might imply a responsibility to assemble for critical view all indices that have been proposed by anyone anywhere.

Many varieties of indices have been invented for many practical ecological situations. Published accounts are scattered widely in many journals and report series. Some have never been formally published but are nevertheless in use. Several man years of literary and laboratory search would be necessary to assemble and critically review 90 percent of those now extant. Meanwhile more are being invented. Comprehensiveness was out of the question, hence we decided to offer as examples analyses of a number of classes of indices to illustrate the current state of the art.

(ii) We judged that the second term in our references was of primary significance. Our guidelines ultimately take the form of a series of screens by which ecological insights and information can be selected for particular needs of decision-makers. In mathematical terms, our proposal is analogous to a "transformation" from ecological conceptual space into a decision-maker's practical space.

(iii) We have sketched a number of types of new indices for further research and testing, and have shown how a systematic search might be undertaken for concepts and models from which other new indices could be developed.

(iv) The fourth term has been met partly implicitly in our proposals for screening and division of labour. In addition we have discussed more explicitly how cost of index use may be minimized.

(v) In a sense the whole report is a framework for the fifth term. But we have also made a number of specific recommendations.

Taken together, all terms have been addressed. None were treated exhaustively. Our report is a description of the state-of-the-art combined with a suggested framework for a major mobilization programme for syntheses and transfer into practice of recent scientific advances. We are confident that much could now be achieved from such a programme.

The Working Party recognizes some truth in the statement that "monetary information tends to drive out of circulation quantitative information of greater significance, and quantitative information of any kind tends to retard the circulation of qualitative information" (Gross 1966). We urge against any widespread excessive zeal in developing and applying quantitative measures of any kind. Nevertheless more and better quantification of information is urgently needed.

2. GENERAL SUMMARY AND RECOMMENDATIONS

We interpreted our terms of reference to mean that our attention should focus on tactical operational levels of planning and decision-making. That is, that we should be concerned with the process of identifying variables of use in discussing, selecting, monitoring or modifying activities and processes related to the management of aquatic resources. Following Jantsch's (1972) model of creative action in scientific management, as shown in Figure 2.1, we have addressed most directly the second box of the lowest tier, labelled "systemic variables", particularly those which may be called ecological variables.

In accounting for the work of our group we wish to address those readers having primary responsibility for strategic planning, i.e., for the second box of the second tier of Figure 2.1. We wish to call attention to developments in ecological science which are needed to increase the variety and effectiveness of management tactics in aquatic resources.

The special role of science in environmental management is not made explicit in Figure 2.1. To date, ecological sciences particularly relevant to environmental and renewable resource issues have been developed mainly with respect to the demands of the lowest tier, that is, tactical operations. Within larger, highly developed countries, scientifically competent people can be found to deal with each box and arrow of the model. Various initiatives have been taken, especially under UNEP, IUCN, ICSU, Unesco, FAO and other international agencies to develop an understanding of and a social process for all the elements of Figure 2.1 that relate "operations" to "values".

At present, however, conceptual frameworks which would permit easy communication among these elements are still poorly formed. Within ecological science itself there remain great difficulties in linking together the specific competencies of the many disciplines composing ecology to meet resource management needs. In this report we focus primarily on this latter problem.

Section 1 contains our terms of reference and a brief account of our experiences in dealing with them. Section 3 develops a rationale according to which the plethora of theoretical, methodological and practical initiatives of environmental and resource scientists might be mobilized for more effective transfer of science into practice. Technical appendixes of Section 4 take up in greater depth certain matters raised in Section 3. The bibliography of Section 5 could readily have been increased to five times its length and serves to illustrate that much scientific work is currently underway on these general issues.

As a result of its deliberations, our working party concludes that management of aquatic environments to enhance resources would now benefit from a direct initiative to organize, mobilize and transfer knowledge related to the needs of detecting, diagnosing, forecasting and controlling man-caused "anthropogenic" stresses on aquatic systems.

The time seems appropriate for such an initiative. What is needed in the first instance is an efficient and effective common framework shared by scientists and users. The framework should be pragmatic rather than doctrinaire in essence. We have proposed such a framework in Section 3; alternatives, currently unknown to us, may already exist.

Extensive coordinated programmes of field testing and experimentation would now be premature. Some general synthesis should first be attempted using expertise, scientific insights and data currently already available. Costs of synthesis need not be large. The primary requirement is that several scores of competent well-rounded scientists be recruited into a loosely-organized but well-coordinated international network and be granted adequate but modest resources to get on with the task. We emphasize that synthesis should be attempted explicitly with respect to one or more pragmatically useful frameworks. We guess that five years might be more than sufficient for this phase.

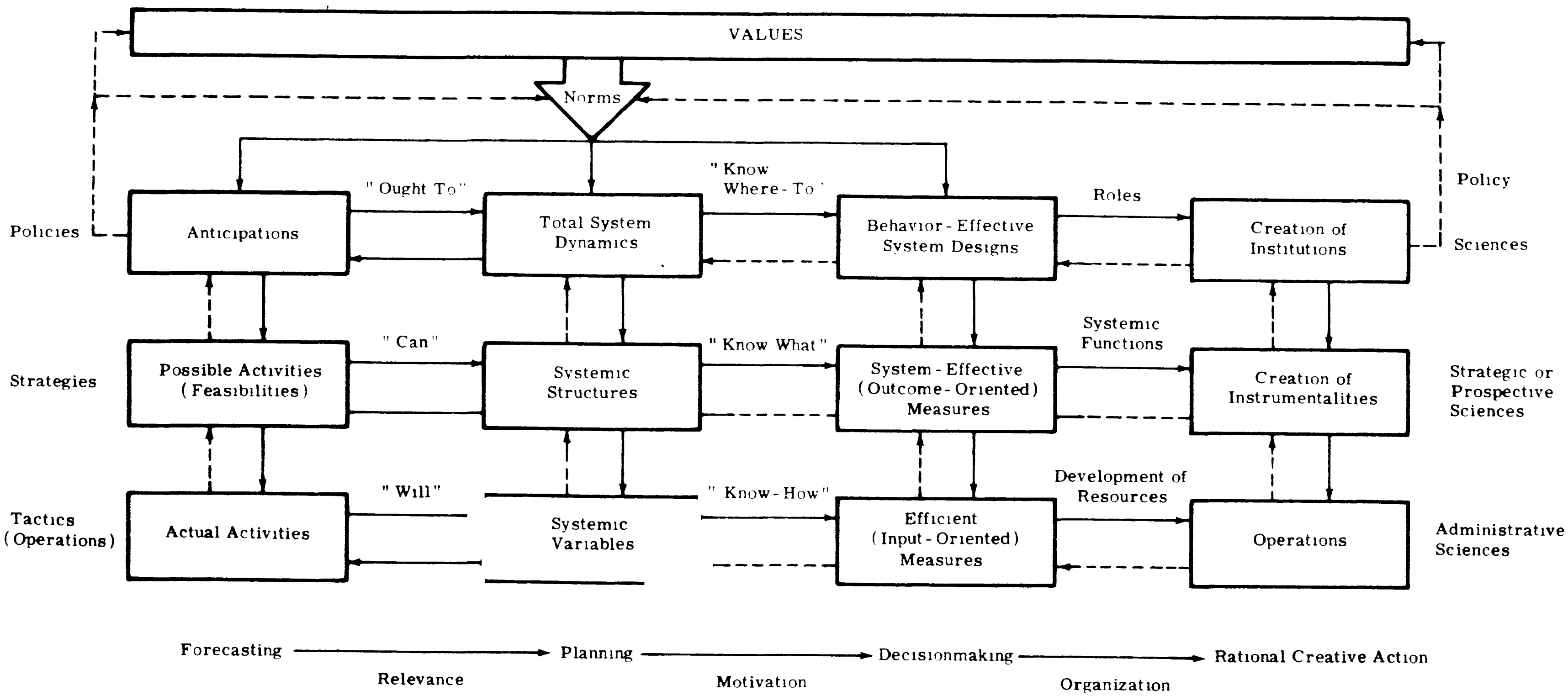

Figure 2.1 An idealized model of "structured rationalization of creative action" by Jantsch. (Jantsch, Erich: 'Technological Planning and Social Futures', London 1972)

Given that a measure of useful synthesis can be achieved with respect to a user-scientist framework, then much of the future ecological work and field testing will inevitably be related to that framework. Some order - but hopefully not order to an excessive and sterile degree - will emerge in what now appears as a relatively chaotic and hectic mélange of scientific initiatives and activities.

More specifically, we recommend the following as sequels to our working party's activities:

2.1 Our report should be distributed to appropriate officers and scientists in:

- the UN system of Specialized Agencies' programmes coordinated through UNEP;
- the International Union for the Conservation of Nature, IUCN;
- the International Council of Scientific Unions, ICSU; and
- regional international fisheries committees and commissions.

2.2 Two separate multidisciplinary panels should be convened in 1976-77 to propose efficient and sufficient scientific approaches to:

- high-impact high-variability phenomena as influencing aquatic renewable resources;
- low-level long-term stresses that have insidious and chronic effects on the resources.

2.3 An international symposium should be convened in 1978, desirably in cooperation with IABO and with INTECOL's Second International Ecological Congress to bring together theoretical and experience papers and contribute to our recommended synthesis. If the two multidisciplinary panels proposed above will have endorsed the framework proposed in our present report, then that framework should be used explicitly to help structure the 1978 symposium.

2.4 Beginning in 1978, the results of work by us, by the proposed trans-disciplinary panels and by the international symposium augmented by the numerous activities of other groups proceeding more or less independently of the FAO/UNEP programme should be used as a basis for proposing major international field testing of systems of indices to measure anthropogenic stress effects on aquatic renewable resources, and for developing practical manuals on that subject.

2.5 A need for more long term "baseline" studies including data on major aquatic ecosystems and their biological composition and structure, continues to lie at the base of the general problem of lack of understanding of problems of resource utilization and management. Such work is often unpopular both with scientists and funding agencies, owing to its routine nature, however, we urge that due consideration and encouragement be given by FAO, UNEP, Unesco and other such Agencies to work of this type.

3. TECHNICAL SECTION

3.1 Introduction

3.1.1 Indices: Roles within Scientific Information Systems

Scientific research and data-gathering processes related to man's interests in aquatic renewable resources have expanded rapidly in recent years. A number of complementary initiatives can be identified:

(a) Monitoring or surveillance of important human uses of and effects on the resource system to assemble data needed for regulation of harvesting, material loading, physical modifications and the introduction of exotic species.

(b) Mapping the spatial distribution of resources and user effects in order for example to determine the rights to specific resources and assign credit or blame for enhancement or reduction of resource productivity.

(c) Modelling explicitly the separate and joint effects of a number of uses in order perhaps to assign fair user charges and thus to internalize costs within the enterprise or agency that have in the past been externalized to society as a whole.

(d) Assessing, i.e., evaluating with the aid of all appropriate data and insights from mapping, monitoring and modelling, the likely ecological impact of a proposed innovation or development to determine whether it should proceed and if so under what constraints.

Ecological indices, as defined below, could be incorporated within all four initiatives stated above - there is nothing about indices *per se* to invalidate their widespread application. But as a practical matter, they are most commonly and most naturally applied in monitoring - secondarily in mapping and in connexion with impact assessment. And it appears clear that ACMRR intended that such should be our interpretation.

We emphasize that the four initiatives specified above are not independent conceptually, but instead are complementary within both the scientists' and decision-makers' viewpoints. Thus if we focus here primarily on indices useful for monitoring, we do realize that to be helpful in the long run our findings will need generally to conform with concurrent advancements in mapping, modelling and assessing.

3.1.2 What is an index?

3.1.2.1 Definition

For our purposes an index is taken as a variable which measures the response of a system (a population, community or ecosystem) to some stress or stimulus, or which measures the stimulus itself. Given a sewage outfall to a river (the system), a great variety of responses (e.g., fish kill, odour, septic water) may result from excessive discharge (the stimulus). Various indices or measures could be defined to relate observation to a selected response, such as a fish kill. These indices might be direct (numbers of dead fish, fraction of original population killed), or, with more knowledge of underlying causal processes, might be measures of intermediate or related factors such as the concentration of oxygen at selected stations. Similarly such indices as COD, BOD and coliform count may be selected along with measures of volume discharge to represent the intensity of stimulus.

The selection of indices in relation to such problems may be regarded as a two-stage process, involving first the selection of stimulus-response factors appropriate to the problem and secondly the selection of appropriate measures of these factors.

The essential formal characteristics of indices can be explained in relation to an ideal case where R, a quantifiable response, is some function, f, of a quantifiable stimulus, S, that is:

$$R = f(S)$$

An index of response is selected such that a given level of response determines a definite value of the index. The response is thus represented by an index, I_r, as a function, g, of the response.

$$I_r = g(R)$$

Similarly an index of the stimulus, I_s, may be selected so that

$$I_s = h(S)$$

Since $R = f(S)$, $I_r = g(f(S))$,

that is, the index of response is also determined by the value of the stimulus. In practice, it will often happen that the magnitude of the response is not uniquely determined by a specified level of stimulus owing to variability characteristic of biological systems. Similarly, the value of an index may be subject to errors of observation and not uniquely determined by the factor it purports to measure. Further, several levels of stimulus may yield the same response, or a single value of an index may result from several levels of an observed factor. These complications may severely limit the strength of an inference which attempts to identify the cause (stimulus) of an observed response.

3.1.2.2 Simple and complex indices

Busy decision-makers and the public-at-large prefer to deal with formulations that are simple numerically or graphically. Thus the search for measurable characteristics of stimuli and responses is usually focused on simple indices and simple functional relationships. Though rather complex mechanisms may be known to underlie ecological interactions, a simple rationalization should be sought at the outset which may well satisfy the decision-maker, if not the scientist trying to gain deeper understanding of the operation of the system in question. The fate of such simple formulations (Figure 3.1) will be determined by their practical performance.

With more understanding of a particular system, more complex indices relating to sets of stimuli and responses may be derived in the form of sums, products, vectors or matrices. Complex indices derived from observations of several factors will usually be most informative if they are not aggregated into single numbers, though simplicity for the user may sometimes justify such usage (see Appendix 4.6).

3.1.2.3 Detection, diagnosis, control, assessment and prevention

Indices may be used simply to provide general information on the status of the environment and aquatic resources and on the existence of trends. If the purpose is to detect whether man's activities are having some effect, then standard baselines and background trends must be taken into consideration explicitly. Quite simple monitoring or periodic mapping programmes may suffice for this purpose.

Sets of indices may be developed to help identify the factors or stimuli that have caused a particular environmental effect or response. The way in which physicians use such measures as blood pressure; body temperature, skin condition and urine composition to diagnose illness is analogous to what is being developed for broad ecological application.

A specified stress factor may be controllable at or near its source by technological means. Indices may be applied to monitor the degree of success of the control process or regulatory regime. Simple monitoring programmes may be devised for these purposes.

- INDICES
  - STIMULUS
    - SINGLE
      - concentration of a specific fertilizer
      - thermal input
      - biocides such as herbicides and pesticides
      - suspended solids
    - COMPLEX
      - industrial effluents
      - oil
      - radionuclides
  - RESPONSE
    - SINGLE
      - BOD
      - primary production
      - indicator species
      - bioassay LD_{50}
      - natural growth
      - reproduction and mortality
      - population yield
    - COMPLEX
      - COMMUNITY
        - diversity
        - space and time patterns
        - species grouping
        - total yield
        - "stress succession"
      - ECOSYSTEM
        - ratios, e.g., production/respiration
        - structure/maintenance
        - producer/consumer
        - energy pathways and delays

Figure 3.1 Classification of different types of indices

Technological developments invariably cause changes in the environment, some of which are desirable and others not. Planning new developments often requires that likely impacts be assessed beforehand. Some quantitative understanding of ecological processes is essential and developments of useful indices may well involve some statistical or more sophisticated modelling.

Even more understanding is required if decision-makers request predictions, perhaps in order to consider major policy changes. Major causal mechanisms should be understood and incorporated if possible into a dynamic model. The model may then be analysed to provide efficient and sufficient indices that should prove useful in monitoring any new initiatives of the decision-maker (see Section 3.3.1.3 for further details).

Models of this sort impose special requirements on sampling and monitoring. The model is not only a specification of which measurements are needed (Schindler 1973, Wulff 1976). Simultaneous observations of the selected variables are required, at intervals of space and time appropriate to the model, for dynamic representations (see 3.3.2.2; 3.3.2.5).

3.1.3 Desirable characteristics of indices

As implied above, the definition of an index derives from some understanding of the response of a system to stimulus, stress, impact or perturbing influence. In that it is a simplified, condensed form of our understanding it may be termed a "stripped-down model" because factors of secondary importance are intentionally deleted. Practical relevance and high scientific precision are often incompatible goals, but indices of low relevance and precision can be misleading and worse than useless. Indices are intended to serve practical purposes in the first instance, thus informed judgement is essential.

The index of the system's ecological response should be a linear of simple curvilinear function over the range of those aspects of the ecological response that are of direct interest to the decision-maker; similarly for the interrelationship of stimulus index and actual stimulus process, and of the two indices to each other.

If the effect of a particular stress factor is to be monitored or assessed, clearly the index or indices to be used must be capable of discriminating between that particular effect and natural background "noise" as well as other stresses' effects.

3.1.4 Meeting the user's needs

Most ecologists perceive their systems to be highly complex. Those scientists who expect confidently that nature's laws are basically simple continue to hope for a major theoretical breakthrough that will lead to simple yet comprehensively useful conceptualizations. Whether or not this is a realistic expectation for the long term, in the short term most ecologists perceive reality in a complex way. Thus their present data needs are also complex as are the methods for processing, analysing and condensing them.

When advising management personnel, especially if time is short and resources are limited, the scientist should not be concerned primarily with how many data are needed to write a thesis, but how few are needed to meet the user's needs. But in resolving this potential conflict there is a moral obligation upon the scientist to ensure that his answers and advice have scientific integrity throughout.

Consider the following example. An industrial operator with a point source effluent discharge needs realistic measures of the ecological effects of his discharges to decide whether something should be done about them.

The assessment may be phased in a stepwise manner.

Question 1 - "Does the effluent discharge have a detectable ecological effect? Yes or no?" Sometimes simple data will lead to a firm answer of 'Yes'. These might relate to the stimulus, for example, the known presence of toxic material in the discharge. Alternatively they might relate to the response, for example, the number of species in an area near the discharge compared with the number in an equivalent, more distant area.

The danger in replying to the original question lies in the 'No' alternative. Here, elements of probability should normally be introduced and a suitable answer might be "Probably no, but at this time I cannot give a definite answer". Industrial operators should be made aware of the dangers of forcing a definite 'No' answer from an ecologist and this being disproved by events. This applies particularly to effluents that might have sub-lethal or cumulative effects.

In the event of a 'Yes' answer the following further questions might be posed.

Question 2 - "How large is the area affected, in relation to the magnitude of the discharge and the scale of the receiving system? Large, medium, or small?" Mapping is required. A degree of subjectivity is involved demanding some practical sophistication on the part of the ecologist.

Question 3 - "Within the area of detected effect, is the damage or change severe, moderate or slight?" Estimates of the intensity of ecological response are needed.

Question 4 - "Are other users of the aquatic system benefiting or suffering from the consequences of these discharges?" The major interactions with other users, mediated through the ecological system, must be assessed.

Question 5 - "If we try to mitigate these effects what are the ecological implications of the various options?" Any reply is likely again to involve probabilities, and possibly value judgements on the degrees of acceptability of the ecological effects.

Further monitoring and periodic assessment must be suggested.

If the above sequence is approximately what does or should happen in industrial and political decision-making these days, it is important to note that although a full evaluation of ecological effects has not been required, considerable ecological understanding may be implicit, even to answer question 1. The more complete and precise this understanding is and the more it relates to the practical concern the more reliable the answers to the questions will be.

We emphasize that direct and early collaboration between ecologist and manager or administrator greatly facilitates the development of useful insights and information on all sides.

3.2 Ecological considerations

3.2.1 Ecological science

"Ecology" is occasionally used as a term of such generality as to be only one level below that of cosmology. Others might limit the term to encompass only three functional relationships defined for a particular species or stock: growth rate, natural mortality rate, and a stock-recruitment function. In our use we shall steer well clear of such extremes.

The ecological theorist may perceive in our approach a leaning toward concepts such as the following. An ecological system develops self-regulatory capabilities to the extent that these do not seriously constrain the system in adjusting to the normal vagaries and vicissitudes of external factors. Ecological systems can be modelled to a useful degree using a relatively small number of factors and highly aggregated components. Natural as

well as human or anthropogenic stresses can be classified into a small number of generalized types to each of which ecosystems tend to respond in a similar manner and from each of which ecosystems tend to recover in a standard manner following a relaxation of stress. Over long periods of time system parameters tend to change due to biological evolution, geological processes, climatic shifts, etc.

3.2.2 Aquatic biomes

Analysing our terms of reference from another perspective, four biomes (classes of aquatic ecosystems) are of particular interest: offshore marine, shelf seas, brackish plus estuarial, and freshwater. Practical pollution problems are currently most intense with some freshwater systems near major conurbations; with some exceptions, pollution tends to be less intense the further one moves from human settlements and/or the closer one moves to the centres of the open oceans.

Each of the four aquatic biomes has traditionally been disaggregated into more than five major classes plus minor classes of aquatic ecosystems (see textbooks in limnology and marine ecology). Clearly to attempt to devise sets of unique ecological indices for each of the common types of aquatic ecosystem would be expensive folly. We seek indices most of which will be applicable to many if not most of the ecosystem types. Each index may well have to be calibrated or "coarse tuned" for a particular type and eventually "fine tuned" for a particular application.

3.2.3 Typical biotopes

Four broad categories of biotopes exist within aquatic ecosystems: the two main types of benthic communities associated respectively with hard or soft substrate and the planktonic and nektonic division of the pelagial communities living in the water column.

Benthic life consists of attached, slow-moving or burrowing organisms with their related and dependent species. They are organized in various 2- or 3-dimensional modes with various emphases upon fixed or relatively static spatial relationships. Pelagial systems, by contrast, are organized as mobile units of spatial-temporal sequences, the scale and range of which are much greater in the larger and more powerfully swimming nekton than in the plankton.

Such classification does not imply that basic biological properties and functions are markedly different in these four biotopes. Rather it recognizes that in attempting to use indices, practical questions may arise that spring directly from the spatial/temporal pattern and scale of organization of the community concerned. The task of developing four sets of indices - not necessarily unique - and calibrating them to an approximate though useful degree, is clearly less daunting than developing a set of indices for each of some 20 or more classes of aquatic ecosystems.

We note that the approach sketched in this section is consistent with the instruction in our charge to place special emphasis on community indices.

3.2.4 Community and ecosystem properties

The concept of system properties (or behaviour, or response) is inherently accepted in some form by most biologists. Where biological units can be grouped into a larger unit, the larger unit will have a collective behaviour, and a collective response to a stimulus.

Our working hypotheses are: that there are system responses that must be observed or sought at the community level to be discovered, that these responses are not predictable in a simple way from observing just the actions or interactions of lower level components, and that the community system responses themselves must be directly observed (Kerr 1974, Pattee 1970).

Application of indices at the community level will require that community responses be identified, and that these properties be related to environmental quality concerns.

Slow progress in community index research is likely if considerable effort is spent on attempts to synthesize community responses from units at the population and individual hierarchical levels before the fact of identifying the response empirically at the community level. The problem has sometimes been perceived as mapping the action of a single independent stress factor onto a two-species, or n-species system. As an example, people with a population background in fisheries may try to approach community exploitation by fisheries as a multi-population problem. Little headway has been made by this approach, though the problem has been well recognized for over 15 years. There is confusion in regard to multi-species fisheries because it is difficult to make hypotheses about the simultaneous action of a fishing fleet on several species, some of which are food for others. We suggest that it is often better to detect empirically a holistic response of some part of the system in which fishes are embedded, rather than attempt to anticipate this response by forcing population models together (Regier and Loftus 1972).

It is partially for the same reason that we have difficulty in dealing effectively with "environmental contaminants". It is difficult to make hypotheses on a multi-population basis. We suggest that the problem be attacked more strongly at the hierarchical level in which assemblages are units rather than species and populations. It is in retrospect that community responses can be explained by autecology.

Examples of macroscale behaviours that may be worth study are resilience, persistence, succession, minimization of nutrient loss and maximization of energy delay in the system. (Further examples are given in Figure 3.1 and Table 3.1.) The first three have analogous counterparts at the population level; e.g., population growth may be thought of as an analogue of community succession, if succession is viewed as a cycle that includes a major perturbation, and if it is realized that populations may cycle on the basis of internal variables alone (see Appendix 4.7). Nutrient conservation and energy delay do not have population counterparts because different species have different trade-off strategies with regard to energy and nutrient use.

3.2.5 Difficulties with community and ecosystem approaches

The injunction in our terms of reference to place particular emphasis upon communities does not prevent us recognizing limitations or difficulties that may exist at that level. Side-stepping the futility of attempting to define "community" it remains probable that many ecologists would include some element of species interactions within their concept of community. But types and degrees of interaction are highly variable, and some species - perhaps because of their abundance but more probably because of their size, form or role in the community - exert much more influence than other species on the overall character of the community (Dayton 1971, Tyler 1974). Such "key species" or "foundation species" are exemplified by those cold temperate forests where much of the system can be determined by a few species of trees, each individual of which influences the same area for many years.

The mobile nature of much of the environment precludes the possibility of spatial and structural dominance of this type in pelagial systems. But the spatial/temporal component is evident in some benthic communities where the more stable sediments and rocky substrata afford sites for ground-cover species that are attached or relatively immobile, e.g., bivalves, tubicolous polychaetes and crustacea in sediment; and algae, sponges, zoanthids, ascidians, barnacles, mussels, and oysters on rock. When established in abundance such species may individually and in diverse ways effectively reduce macro-diversity by excluding other potential macro-users of the same space: on the other hand they may also provide new secondary habitats for an abundance of individuals and of species of small size and short life-span. (Dayton 1971, Lewis 1964 and 1970, Paine 1966, Tyler 1974.)

Since ground-cover species not only compete with each other but are subject to grazing or predation it is frequently the state of the balance between small numbers of interacting species that determines the composition of the community: e.g., echinoids or limpets on

algae; asteroids or whelks on mussels or barnacles; asteroids or nudibranchs on sponges. (Connell 1970, Dayton et al. 1974, Leighton et al. 1966, Lewis 1970, Paine 1974, Sutherland 1974, Southward 1956.)

As a minimum in such cases the degree of species control rather than physical control of the community has to be determined if serious misinterpretation of community data is to be avoided. But taken in conjunction with the practical aspects of data collection on or in the substrata, it is probable that where a few species do dominate all facets of the community such species may provide the most economical means of monitoring that community.

At the community level, the length of time required by an assemblage of populations to complete a response may be very long. Some commercially important aquatic species may take 25 or more years to complete their lives and five or more years to reach harvestable size. Computer simulations of the behaviour of populations have shown time lags of 10 or more years are required before fisheries might expect to feel the beneficial effects of a change in management policies (Hackney and Minns 1974). It would be expected that the responses of the communities or ecosystems of which such populations are a part would require even longer to achieve new equilibrium values.

Even more troublesome is the fact that varying time lags within a system may result in initial responses (transients) which take quite different directions from the final ones (see 3.2.7). Such transient responses are easily confused with long-term "equilibrium" responses in studies.

Another sort of difficulty relates to hypotheses of causal mechanisms at the community level (see section 3.2.4). In single-species fisheries we can make good estimates of the extent of the initial alteration - we have killed so many pounds of fish, we know how to make and test hypotheses about the dynamic consequences and subsequently we can anticipate persistence. In multi-species fisheries we know the alteration, but we may not know how to make hypotheses about the dynamic consequences, and then can make only guesses about persistence of particular species. In multi-species pollution, we may often not even know the extent of the alteration.

We emphasize that population-level indices are often effective and efficient (see Appendixes 4.2, 4.3 and 4.4).

3.2.6 Natural temporal variability

The natural biological background against which the responses to human influences have to be detected is far from stable. Populations, communities and ecosystems change in various ways: directionally, cyclically and on time scales that may range from hours to centuries.

Directional or progressive changes may reflect the natural evolution of a physical environment when, for example, a lake or estuary is gradually filled. Long-term climatic changes, such as the increased temperatures of sub-arctic waters, are basically cyclical but they may appear progressive during our period of knowledge. Biological responses on these scales are manifest in the disappearance of the Baltic herring at the end of fifteenth century (Thurow 1974) and within the fossil record (Hallam 1967, Sheldon 1965). 'Change' is not therefore always attributable to man, and in fact a background must be identified that is relevant to each problem.

On a more immediately relevant level, many cyclical changes are responses to 'normal' levels of abiotic variation that have diurnal, circadian, lunar, seasonal or annual periodicities, and possibly an 11-year cycle related to sun-spot activity. Such biological changes, once they are understood, constitute the most obvious component of 'background noise' that it may be possible to discount thereafter.

But virtually all abiotic factors that influence aquatic life also fluctuate with a degree of irregularity that poses important problems. Species are adapted to the levels of

Table 3.1 A series of variables appropriate for a macroscopic analysis of ecosystem characteristics and processes as interrelated in the context of the succession phenomenon (from Odum 1969). "Succession" here connotes a recovery process following relaxation of a major destructive event or process

Ecosystem variables	Developmental stages	Mature stages
	Community Energetics	
1. Gross production/community respiration (P/R ratio)	Greater or less than 1	Approaches 1
2. Gross production/standing crop biomass (P/B ratio)	High	Low
3. Biomass supported/unit energy flow (B/E ratio)	Low	High
4. Net community production (yield)	High	Low
5. Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
	Community Structure	
6. Total organic matter	Small	Large
7. Inorganic nutrients	Extrabiotic	Intrabiotic
8. Species diversity - variety component	Low	High
9. Species diversity - equitability component	Low	High
10. Biochemical diversity	Low	High
11. Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well organized
	Life History	
12. Niche specialization	Broad	Narrow
13. Size of organism	Small	Large
14. Life cycles	Short, simple	Long, complex
	Nutrient Cycling	
15. Mineral cycles	Open	Closed
16. Nutrient exchange rate, between organisms and environment	Rapid	Slow
17. Role of detritus in nutrient regeneration	Unimportant	Important
	Selection Pressure	
18. Production	Quantity	Quality
	Overall Homeostasis	
19. Internal symbiosis	Undeveloped	Developed
20. Nutrient conservation	Poor	Good
21. Stability (resistance to normal external perturbations)	Poor	Good
22. Entropy	High	Low
23. Information	Low	High

variability that are normally experienced in their own habitat, but the intermittent, more extreme event of, for example, temperature (Crisp 1964), salinity (Hildebrand and Gunter 1953), or flood surge (Stephenson, Williams and Cook 1974) may cause appreciable mortality and entrain a phase of successional recovery.

The more frequent but lesser departures from normal may evoke new responses of feeding activity, growth rate, fecundity and so forth. The consequential changes in the overall competitive efficiency of one species, relative to the others with which there are interactive relationships, may then set in train biological chain reactions that could affect the species composition and spatial patterning of communities for varying durations thereafter. Slight abiotic changes that are unidirectional for one or few decades can lead to progressive changes in the geographical distribution of individual species, and in the composition of communities. Recent changes in the English Channel appear to illustrate this response to a slight climatic trend (Southward et al. 1975).

It follows therefore that no biological measure that we may wish to use for index purposes remains constant. The concept of 'baseline' is misleadingly oversimplified. Rather there are spectra of values which encompass the normal range of responses. Unfortunately neither the amplitude nor the controlling factors are known with accuracy for many species, or communities or for many parts of the world.

The significance of the existence of such background fluctuations is inversely proportional to the severity of any man-made stress that is being investigated. The widespread and severe mortality that may result from a major tanker accident transcends all the subtleties and most of the extremes of natural causalities; but in assessing the effects of a new industrial or urban discharge misinterpretation could arise. Such misinterpretation can best be minimized by initiating studies on the scale of local variability over as long a period as possible before the need for assessment arises. Clearly, early consultation between ecologists and management is required, but the broad-scale exemplary utility of more general baseline data relating especially to the consequences of climatic/hydrographic fluctuations would justify long-term national or international levels of approach rather than the short-term, ad hoc, local plant level.

3.2.7 Lag effects and transients

The practical interpretation of a stimulus-response process must take into account temporal lags that may occur between response and stimulus. A simple hypothetical case is sketched in Figure 3.2. In the top panel the stress regime is depicted as growing gradually and regularly from S_1 to S_2, these corresponding to points A and B in the bottom left panel. Meanwhile a lag in response is occurring which is in part depicted as a curved line of somewhat arbitrary nature. When the stress regime has reached level S_2 some decision is taken to stop any further increase in stress and to hold it constant at S_2. If it remains constant for an adequate length of time the response will eventually equilibrate to level S_2, point C. Often this involves some temporary overshoot, e.g., to C prior to equilibration at C (lower right panel). Subsequently a decision is taken to reduce the stress gradually and regularly to its initial level, D in top panel. Because of lags in the recovery process the response is still appreciably above the initial level D, in bottom panels, when the stimulus achieves its initial level. If the response occurred in a way that no permanent ecological damage was done, then eventually the response will equilibrate at its initial level. This would be a reversible case. When permanent damage has occurred, the recovery process may end at E_1.

To the extent that this simple example has some realism, it suggests some things that should concern the decision-maker. If a stress has been intensifying but then is held constant, a permanent overshoot may nevertheless occur. Also full recovery, if it is ever to occur, may lag many years behind a reduction of stress to initial levels.

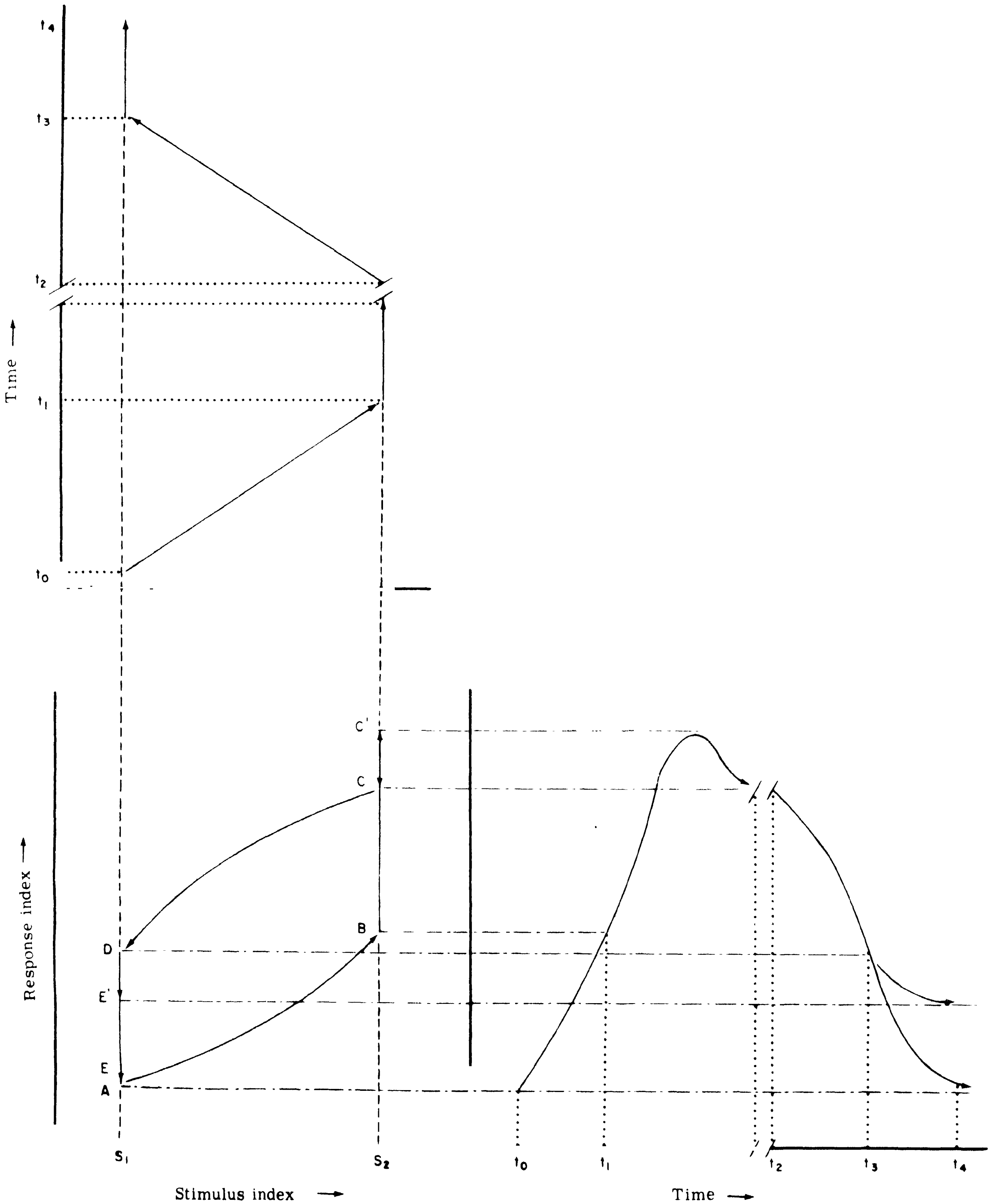

Figure 3.2 Effects of ecological lags and irreversibilities in response to a stimulus regime: a simple hypothetical example. See text.

Figure 3.3 depicts the effect on the fish biota of a part of the Zambezi River, of the construction of the Kariba dam (Balon 1974). The example is more complex than shown in Figure 3.2 in one way in that transient "undershoots" occurred; also the stress was permanent in that the dam was not subsequently removed, of course.

In the Kariba case, some of the overall long-term effects are obtained by comparing the data shown for 1971 (when equilibration was approximately complete) with those for 1957 (prior to dam construction). Long-term effects included increases in total dissolved solids, number of species and gross production of the fish biota.

Between 1958 and 1971 the various indices fluctuated in a non-synchronous manner. In the absence of some general understanding of the usual sequence of events following damming, an investigator would have been seriously in error if he had estimated long-term equilibrium conditions by extrapolating the trends that occurred between 1960 and 1963.

The dashed lines beyond 1971 are predictions of what would occur to the indices if nutrient loading from sewage and farmland runoff occurred as depicted in the bottom right-hand corner. These predictions were based on experiences elsewhere.

3.2.8 Various schools of ecology

Table 3.2 identifies and classifies a number of ecological traditions each of which has demonstrated some involvement with aquatic communities and ecosystems. The list could be extended to include approaches at the organism and population levels such as morphological ecology, physiological ecology, population dynamics, epidemiology, etc.

If each of the various traditions has elaborated quantitative models that have been tested in the standard ways of science, then each could serve as a basis for development of one or more ecological indices. Of course many of the traditions have already taken that step. Only some of the actual or potential indices would relate closely to our present task of identifying indices to measure effects of anthropogenic stresses on aquatic living resources.

The list here provided, modified according to the insights of the informed user, could be a basis for an efficient systematic search of the literature for indices already developed and for conceptual bases for new indices.

3.2.9 A strategic classification

The adverse ecological effects of different industrial, urban and resource developments may vary from almost zero to a number of almost infinite magnitude. Besides the expected or average value of an effect, the impact of temporal and spatial variability patterns is of great practical importance. Following is a sketch of a rationale developed in more detail in Appendix 4.8.

Practical folk take into consideration both the expected value and the variability or uncertainty associated with it. With respect to adverse effects the product of the two factors is a measure of risk.

Figure 3.4 illustrates an attempt to find a transdisciplinary context within which different kinds of development proposals may be classified and from which guidance could be found as to the parameters - and implicitly the models - of primary usefulness.

The two dimensions of Figure 3.4 are: expectation in the statistical sense of expected average impact on the social value of the impacted ecosystems (E); and temporal variability and uncertainty that is associated with the expectation (V). The horizontal and vertical scales are not made quantitatively explicit, but they may be interpreted as extending over eight or more orders of magnitude (base 10). In locating, approximately, various kinds of

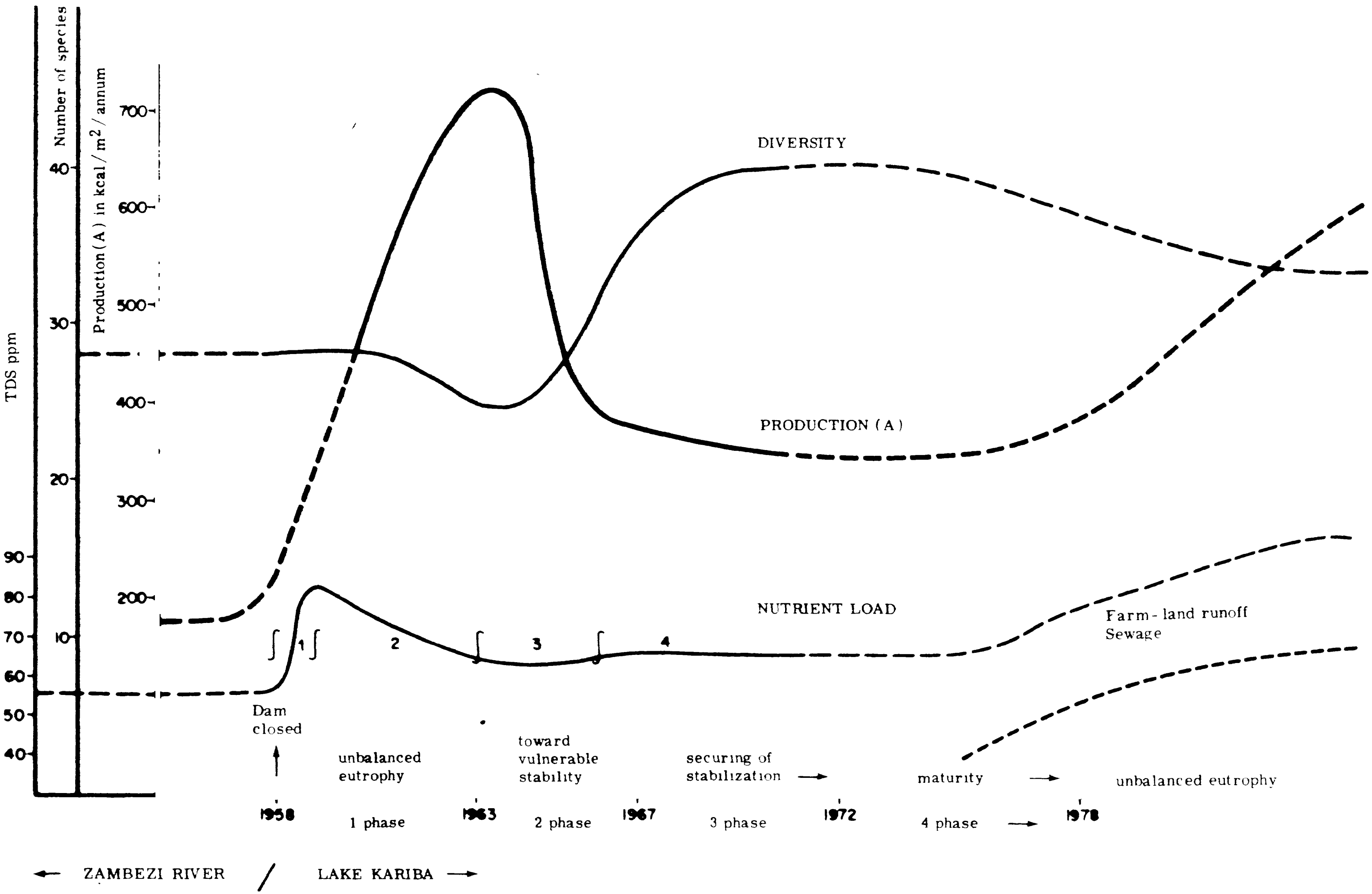

Figure 3.3 Zambezi River prior to impoundment and Lake Kariba history: past, present and future in dynamic variables - nutrient load (TDS in ppm), total fish production (A in kcal/m^2/annum), species diversity (in number of species). Abscissa - years and phases of succession. Chemical phases are marked along the nutrient load line. (From Balon, 1974)

Table 3.2 Ecological traditions within studies of aquatic communities and ecosystems as viewed from a theoretical rather than a practical issue-oriented viewpoint

Structure	Function-Process
1. Whole system classification biotopic typology: Thienemann, Hutchinson, Müller, Moyle, T.A. Stephenson, G. Thorson	Biogeographical processes: Lindsey, MacArthur, Svärdson
2. Whole system abiotic structure, e.g., "morphoedaphics": Rawson, Ryder, Jenkins, Huet, Cuinat	Whole system responses, e.g., "succession" due to sediment in filling of basin: Vollenweider, Rigler, Harvey, Sheldon, Sutcliffe, Regier, Lewis
3. Indicators - species and sub-systems: Saprobensystem: sanitary engineers, Reich	Population dynamics; eutrophication, oligotrophication, and pollution studies: McElreath, Johnson, Brinkhurst, Schindler, Thomas
4. Niche structure: Keast, MacArthur	Natural selection, e.g., interactive segregation: Nilsson, Dodson
5. Trophic pyramids or gross networks: Ryther, Cushing, E.P. Odum	Productivity coefficients and ratios: community metabolism and respiration: H.T. Odum, H. Welch
6. Complicated food webs: Isaacs, Tyler	Trophodynamics, energy and material transfer coefficients: IBP studies, Steele, Dickie, Parsons
7. "Balance", biomass ratios: Swingle, Anderson	Interactions between taxonomic groups: Brooks, Hrbáček, Shapiro
8. Pattern distribution and species associations: W. Stephenson	Species interactions: Lewis, Paine, Connell, Gallucci
9. Diversity/complexity: Pielou, Sanders, MacArthur	Stability/resilience: Holling/Jones, Margalef
10. Particle size profiles: Sheldon	Particle size dynamics: Kerr

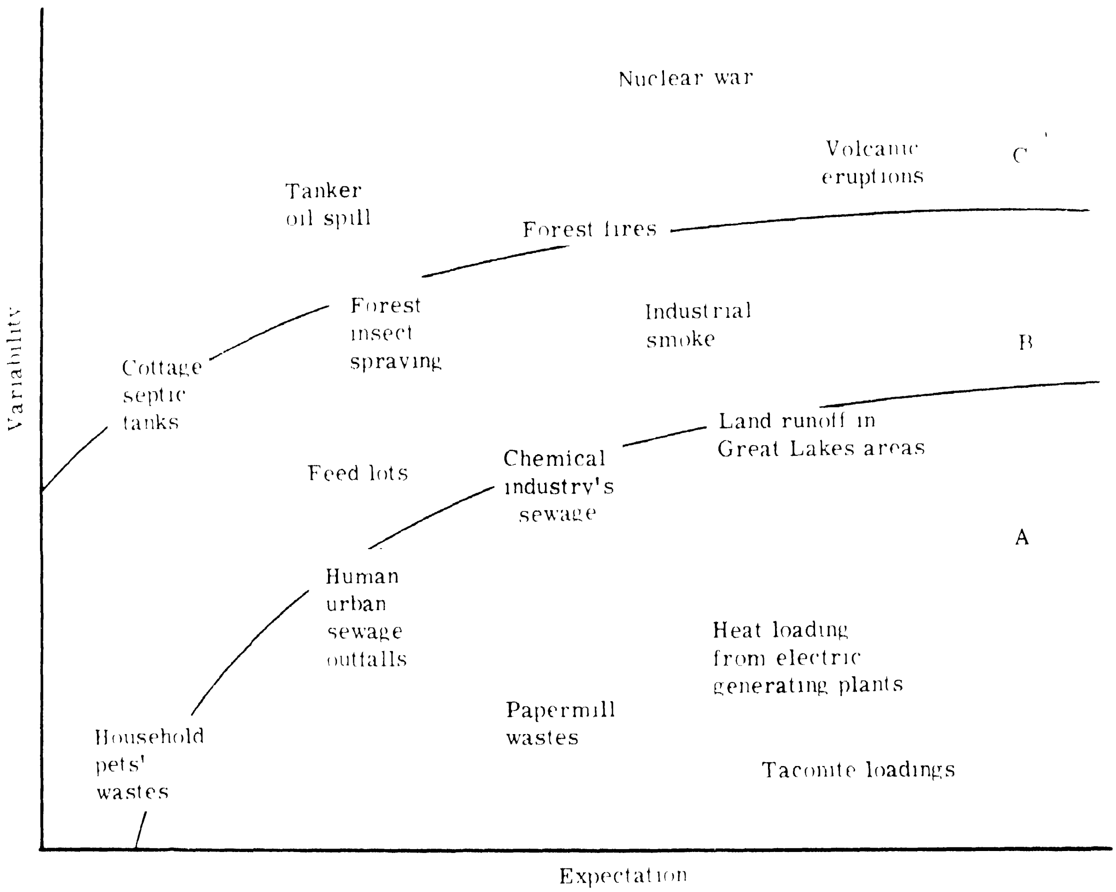

Figure 3.4 Expository model showing the approximate relative significance (in Canada) of expected or average effects (E) and the temporal variability or uncertainty of those effects (V) with various kinds of pollutant loadings. E and V are variables of primary interest to practical decision-makers. Differences in the tactics employed to deal with different kinds of loadings may be rationalized in this context as shown in the text.

impacts the axes have been scaled logarithmically. The location of various stresses in the figure were intended to depict characteristics of those typical of Central Canada and are less realistic for other regions. At best the summary is semi-quantitative, and it should be viewed as an expository framework, at the present time.

The variability axis relates to either or both the temporal variability of the anthropogenic factors (e.g., "pollution") and the temporal variability in the ecosystem variables of special social interest that are closely affected by the anthropogenic influences.

Considering first the margins of the E by V space, developments with high impact fall to the far right and will inevitably be addressed singly and intensively. Low impact developments at the left will often be treated in concert with other low impact developments. At the bottom where variability is low the scope for the neat technological fix is maximal. At the top, the primary concern is to forestall disasters, or to forewarn of impending disasters, or to pick up the pieces after a catastrophe.

The above should not be read as though it were a prescription; it is intended as an inference. Whatever the discipline - ecology, economics, sociology, geography, political science, epidemiology - workers have already developed different models and practical proposals to deal with such differences in expectation and variability. There is a hope - shored up by some preliminary scholarship - that for different subsets of E by V space the various disciplines already have approximate models that are congruent across disciplines. If these commonalities can be identified we will in effect possess a core for an environmental science (include renewable resource science) discipline. But this is tangential to our present purposes.

What has preceded is an attempt to generalize very broadly over the approaches and models used by numerous disciplines to deal with various combinations of average values plus fluctuations and uncertainties in practically useful ways. But human political institutions have not been developed primarily along these lines, but rather with respect to hierarchically nested sets of usually contiguous geographic areas.

With notable exceptions, the lowest level of government deals with the smallest level of area, and has primary responsibility for rather small resources and stress effects. Further, among these the more uncertain or variable aspects may be delegated or reserved for higher authority (Figure 3.5).

The second level, here taken as a sub-national region, has primary responsibility for larger stress effects and also commonly exercises general supervisory responsibility over lower level activities. A similar statement applies to the next level, the national.

At the international level, primary responsibility is of course still vested in national bodies. Decision-making under these circumstances is very difficult, the demands on scientific assistance are intense, but adequate funding for research seldom occurs. We address this point in our recommendation.

Our inferences, as depicted in Figure 3.5 show that major human political institutions are in large measure organized independently to the way that the scientific intellectuals of various disciplines have developed congruent concepts. Consistent with this point is the experience of governments of many kinds during the past decade in that they had to bridge the usual hierarchic levels in order to deal effectively with environmental and renewable resource issues.

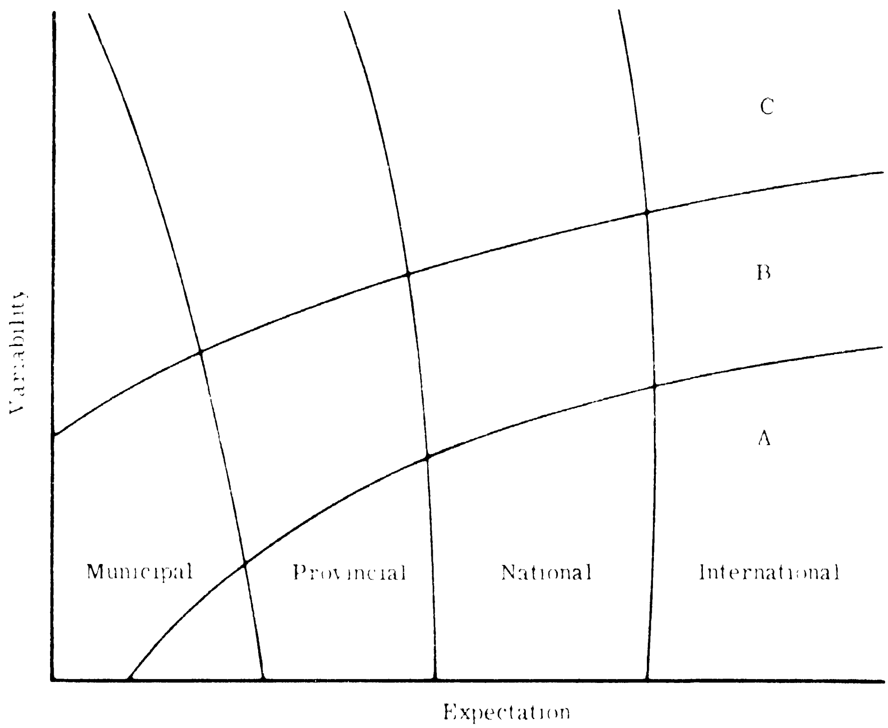

Figure 3.5 The relationship of different levels of jurisdictional responsibility and the three generalized levels of conceptual science. A, B, and C are as shown in Figure 3.4

3.3 Statistical experimental and analytical aspects

3.3.1 Statistical and experimental designs

3.3.1.1 Treatment and control

Identification and eventual evaluation of ecological changes due to human activities involve comparisons between two sets of circumstances: not stressed - the "control"; stressed - the "treatment". A number of alternatives are used commonly, in ecological as well as other fields of science.

(a) In lieu of a control, before and after studies in the affected system are often used in a stimulus-response setting. More comprehensive scientific attempts may be termed perturbation analyses. The methodology of time series analysis (see below) deals with the difficult temporal aspects of sampling. Much of fisheries science is implicitly of this type.

(b) Coincident comparison of affected (treatment) and non-affected (control) systems frequently involve analysis of variance particularly if replication is involved. Spatial aspects of sampling have long concerned ecologists in particular (see below). Statistical aspects of study design have been well developed by agricultural scientists.

(c) Focal point and gradient studies are involved where the site of the discharge is most affected (by the treatment) and points along radii from that point are less affected until eventually unaffected (control) points are found. Initially these may rely on covariance and regression analyses. Sophisticated "focal point studies" may well involve hypotheses of cause and effect and complicated modelling including dynamic simulation and often termed "systems analysis", though we prefer to reserve the latter term for a broader purpose.

Combinations of two or all three of the above ((a), (b), (c)) may be used, particularly if high reliability of advice is a concern.

3.3.1.2 Experimentation and simulation

Together with any of the field study designs specified above, workers may undertake some field experiments of restricted scope, small-scale laboratory simulations and experiments with living material, and numerical or computer simulations using quantitative abstractions based on partial understanding of the system and responses.

Parenthetically we note that the commonly held view that regards laboratory studies as more useful and definitive than field studies is erroneous. The two kinds of work complement each other. Laboratory experiments show what nature can do while field studies demonstrate what nature actually does.

3.3.1.3 Development of an index

In the long term the most effective and efficient system of indices will contain those developed from a comprehensive and intensive understanding of the causal mechanisms that relate response type to the stimulus type. Usually these are developed from the *ad hoc* indices formulated in the early stages of the study of a particular problem. The development and application of indices should include most of the following steps:

(a) Marshalling of insights concerning the stimulus-response system under study.

(b) Application of pre-existing indices that are sufficiently general in their nature that immediate application can be made.

(c) Rapid development of new indices on an ad hoc trial basis.

(d) Empirical observation of new community responses or properties, including initiation of statistical studies to develop correlations and causal hypotheses.

(e) Synthesis of the hypotheses into a larger conceptual framework, i.e., modelling in the broadest sense. Computer simulations are likely to be valuable at this stage to explore the dynamics of causal hypotheses. Sensitivity analyses can be conducted with the simulations in order to rank state variables by degree of anticipated dynamic influence.

(f) New indices can be formulated from the models. In a sense, simulations and other models may be abstracted into indices.

(g) If computer simulation models have been developed, the new indices may be tested on the dynamics of the simulation. The cost-structure of index application may be modelled and added to the simulation, and a benefit-cost analysis may be done.

(h) New indices developed through conceptual processes should be field-tested. At this stage iterations are desirable, and the investigation may want to return to steps, (a), (d) through (h).

3.3.1.4 Cost effectiveness

The greater the risk associated with a projected development involving ecological stress the more likely that experimentation and simulation will be cost-effective when undertaken to complement field studies using such indices as are already reasonably well understood.

Given that: (a) each index of a set of indices has been developed to the point that it is an acceptable measure of the effects of stress on a particular community, (b) that each of the indices measures a somewhat different aspect of response, and (c) that the costs attached to the application of each index are unique, then how does one decide whether application of one subset of these indices would be preferred to another where budget is a management factor?

One way to deal with this problem is through use of a model of the stressed system. Simulated stresses may be applied to the model. The manager himself can exercise the model in a gaming mode, applying first one, then another subset of indices. With each run he can score himself on his ability to make a management decision with a particular index subset by counting the number of simulated hours or days required for stress detection, the simulated cost of index application, the level of pollutant reached before a management decision was made, and the full degree of degradation that had occurred in the system at the time that the decision was made.

Gaming approaches have been developed for fisheries management (Newell and Newton 1968, Tyler 1974). A model is now being developed for the Fish Commission of Oregon in which the object is to maximize long-term yield, and minimize management costs, by using combinations of catch, effort, pre-recruit, and environmental index data (Tyler, personal communication). As a result of the gaming, the investigator should achieve a tentative ranking of his indices, or index sets, so that some of the trial and error is removed as the monitoring programme is applied to the field.

3.3.2 Analytical aspects

3.3.2.1 Boundaries

Wherever an index is associated with self-regulating properties, consideration should be given to the location or definition of boundaries within which the index applies. Two alternatives are common:

Biotopic: Spatial boundaries are defined in traditional terms of fixed abiotic habitat (e.g., a mud flat, rock outcrop, lake).

Biocoenotic: The conceptual boundaries apply to biotic components of ecosystems or subsystems that wander to some extent and are not fixed in space; the spatial boundaries may shift or come to include a series of different habitats (e.g., floodplain fishes, Sargassum communities).

3.3.2.2 Scope and scale

The decision-maker's approach to a pollution problem varies not only quantitatively but also qualitatively with differences in the temporal, geographical, ecological and social impact of the problem (see section 3.2.9). To an important degree, ecological models and methods must conform quite directly to the conventions of the decision-making system of the jurisdiction involved. Social, political, bureaucratic and industrial systems are organized hierarchically, with questions of larger scope and scale being addressed usually at higher levels of power (recall Figure 3.5) and thus requiring that the science and information be aggregated and interpreted appropriate to the needs of the relevant level.

On the basis of the above consideration we judge that the second of our terms of reference - to propose guidelines for the selection and/or formulation of well-balanced sets of indices - must take into consideration their application at various levels of decision-making. We come back to this matter in Section 3.6.4.

3.3.2.3 Classification

In the absence of a well structured and widely accepted conceptual framework for all of aquatic ecology, no consensus need now be expected on a single, overall way of classifying the various entities and quantities potentially of interest to us here.

Elements should be grouped according to the needs of the situation. Practical concerns frequently relate primarily to particular biological species as renewable resources, hence a biological classification is usually involved. But this need not be the traditional Linnean classification (see Balon 1975, 1975a).

Species relate to habitats that can be identified, and sites can be classified accordingly (Section 3.2.2). Property or harvesting rights are often identified geographically by maps, thus providing another practical basis for a spatial approach to classification.

Also, where temporal (including seasonal) phenomena are important, as is the case in most parts of the world, species and habitat features fluctuate spatially and temporally thus requiring appropriate seasonal "stratification". This is another form of classification.

These three classificatory dimensions may be taken, as a first approximation, to be independent of each other and about equally important within a practical monitoring and assessing context.

3.3.2.4 Patterns

"Pattern" may be used to denote a graphic representation of some temporal, structural, distributional or associative characteristics of one or more species in a community or ecosystem.

A migratory species' relative abundance at a point in space may have a pattern through time, and the methods of time series analyses may be used to characterize the pattern's parameters (see Section 3.3.2.6). Similarly, analyses might show associations of particular species in space (see Appendix 4.1).

In addition to species groupings individual species will often be spatially distributed in ways ranging from many small aggregations to being maximally far apart with random placement occurring somewhere inbetween (see biotic axis in Figure 3.6).

Many probability distributions have been used to describe these spatial arrangements, some of which are listed below. Each distribution has specific parameters, which are mean values, and variances about these means may be calculated. For example,

clumps of animals ..... negative binomial distribution ..... 2 parameters
randomly placed ..... Poisson distribution ..... 1 parameter
placed far apart ..... uniform distribution ..... 1 parameter

The parameters themselves may often be sensitive enough to serve as indicators of change due to stress, especially when a distribution can be related to ecological functions. The more notable feature of species patterns is that they are fundamental to any sampling programme and must be given consideration when the number of samples is balanced with the sample size to be taken.

Another type of complexity involves the great differences in size and behaviour of the organisms of potential practical interest in aquatic ecosystems - from a pathogenic virus to the blue whale. Any practical sampling programme can capture only a fraction of the kinds of organisms present.

The shorter and more irregular the temporal fluctuations, or the larger the range of sizes and mobilities of the organisms present, the more difficult it is to devise reliable sampling programmes. Obtaining unbiased and highly precise estimates of abundance, for example, is always out of the question except for a small number of carefully selected life stages of a few species. "Present or absent" data are more readily obtained for a larger number of taxa.

As stated in the previous section, the sophisticated scientist knows that his perception of reality is much influenced by the characteristics of his sampling devices. This is true for all of science, of course.

The potential usefulness of pattern summaries is high. In an ecosystem subject to continued waste loading, replacement in a particular area of one species group by another may be a sensitive measure of response. Thus the outer edge of significant ecological impact may be discerned. The spatial-temporal pattern of a species' cohort - its space-time trajectory - may be influenced by loadings in a way that might readily be discerned using standard sampling gear.

3.3.2.5 Organization in space and time

There are a wide variety of factors and variables which may be used to specify uniqueness of particular ecological stress-response systems. Two of the most commonly used, as with mapping and monitoring, are spatial and/or temporal structure or pattern as influenced by ecological stress.

In Figure 3.6 some organizational aspects of ecological systems or subsystems are shown with respect to three axes of structural dispersion, each associated with a type or class of observation or measurement. Dispersion is here linked to (a) uniformity in spatial and/or temporal organization of the system elements at one end of a scale, leading through (b) unorganized or unstructured class to (c) highly aggregated and inter-acting subunits at the other end.

Returning to the formal definition of an index as a specified function of stimulus or response (see Section 3.1.2), Figure 3.6 suggests that stimuli (stresses) may be generalized as vectors composed of a (natural) biotic set, a (natural) abiotic set, and a human use or anthropogenic set. The degree of structure inherent in a stimulus (a stress) will

be partly copied into the response, e.g., release of a contaminant at a particular point will produce, at least initially, a localized effect. Such correspondences of structural organization in time and space between the nature of the organization of stimuli (or cause) and that of their associated responses may provide help to the investigator seeking explanation of observed effects.

The interactions of abiotic, biotic and anthropogenic factors, as depicted in Figure 3.6 thus include both intensity and organizational components. Care must be taken that the methods of observation used to assign values to an index do not unduly hide or exaggerate the structural component. The measuring or sampling process may itself be structured (e.g., net selectivity), or may be structured intentionally (systematic sampling). The effect of these, and still other pattern attributes of ecological systems should, indeed must, be considered as a apart of ecological analysis.

3.3.2.6 Time series analysis

Data which are accumulated either to establish a natural baseline or to monitor the responses to a stress will generally be recorded over time and at specific intervals. Both the particular times and the intervals should be carefully chosen so as to record indices during the times when meaningful biotic and abiotic events occur, such as spawning, settling and recruitment (see Appendix 4.3), migration and tidal and temperature extremes.

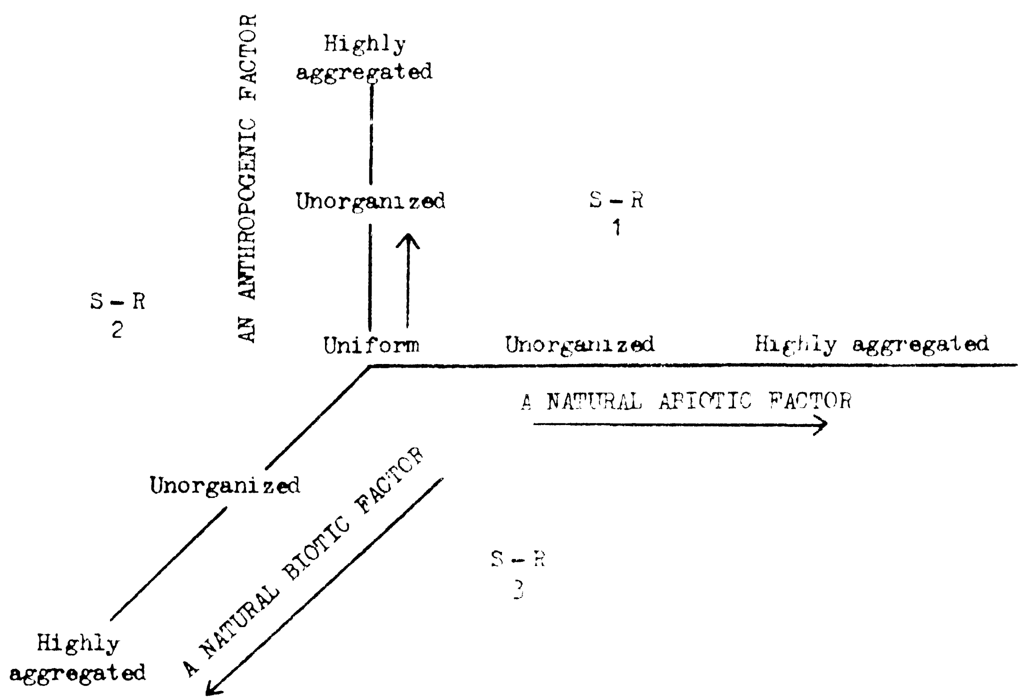

Figure 3.6 Expository model of various organizational relationships which may exist among various factors operating in stimulus-response systems. Specialized statistical methods have been developed, for analysing data in time series and spatial distributions, according to a measure of "dispersion" for which an appropriate mathematical parameter has been defined. Note that S-R 3 is the natural baseline space; S-R 2 is the conceptual space in which direct interactions between stimulus and response of the living community are specified; and S-R 1 contains the influence of the stimulus on the abiotic part of the ecosystem which may subsequently be translated to the biotic via mechanisms within S-R 3.

When data are recorded at equally spaced intervals and when the data sequence spans a long time interval (evaluated with respect to the natural history of the longest lived species of interest) consideration should be given to the application of the statistical methodology of time series analysis.

Time series methods have been highly developed by econometricians (Nelson 1973, Box and Jenkins 1970, Jenkins and Watts 1968) who must cope with cycles, fluctuations and trends in financial indicators. Many ecological indices display both predictable fluctuations and random natural fluctuations, trends and general cyclic behaviour (J. Wildlife Mgmnt. 1954). Furthermore, many indices result from processes that are dependent upon each other. They may be additive or multiplicative or they may be related by being generated by processes which are delayed with respect to each other. For example, harvestable stock lags behind stock size because of the delay between spawning and recruitment. Clearly, indices of system behaviour may be complicated and result from processes that are related by several of the factors acting in concert. Careful analyses will often give insights into how processes relate to each other.

Caddy (1974) applies the methodology in a management study of the scallop fishery, Gallucci (personal communication) to a perch fishery and Gallucci (personal communication) to a study of the relationships between climatic factors and Tussock moth population dynamics.

While the theoretical foundations of the methods are mathematical this need not prevent their use since most sophisticated computer systems now have time series packages in their subprogrammes. Alternatively, several commercial packages are available. A certain degree of skill, acquired by practice or via a statistical consultant, is needed to obtain maximal benefit from the analysis.

Many of the techniques are based on correlations between pairs of sequences of data (cross correlation) or a data sequence within itself (autocorrelation). For example, a sequence of temperatures may be cross correlated with a sequence of community respiration values, both measured at the same times. A positive cross correlation function and a positive autocorrelation function are expected. Each provides information about the processes which generated the indices, viz. community respiration increases with temperature and times of high temperature are usually, for short intervals at least, followed by times of high temperature.

The correlation calculations are one way in which the numerical values of the coefficients in the time series model are evaluated. From analyses such as these, as well as from insights into the processes which generated the indices, a time series model is selected in which the coefficients are used. The model may include explicit terms to account for random variation, delay or lag, oscillation and other dependencies. The model is then run to generate a predicted data set which is statistically compared to the observed data set and the model either accepted or rejected at some pre-set level of significance.

In essence then, one hypothesizes a "grey box" (or partly understood ecosystem) from which sets of indices are emitted over time, generated by processes one knows something about. The indices are sampled to gain sufficient information to construct a model to mimic the real sequence of observations and to make predictions. If a stress is presumed a new grey box is hypothesized (processes or species are modified). The predicted index values from the unstressed system are then compared to the observed index values from the stressed system to determine whether change has occurred.

In conclusion, it should be noted that the methods discussed are largely correlative and thus cause and effect relations, which are often indicated, should not be inferred without further testing.

3.3.2.7 Ecosystem level baselines

Because marine ecosystems are vast and freshwater ecosystems occur in the many millions, and because the work necessary to determine pre-impact baselines is costly, it follows that direct detailed estimates of baselines are out of the question for most aquatic areas of the world. This realization has led to a number of useful initiatives.

One approach is to designate a small number of typical areas to be used as an indicator set for a larger surrounding area. The designation of "biosphere reserves" within Unesco's Man and the Biosphere Programme is an example.

Alternatively a somewhat more comprehensive approach may be attempted based on some insight into the relationship of natural properties of ecosystems to major exogenous variables that are easily measured, or to endogenous variables that can be inexpensively monitored. A randomly selected subset of the areas or ecosystems of interest is studied, relating variables of direct interest but costly to measure to less costly covariates or indices to be used as surrogates. The interrelationships are then determined statistically. If the fit is usefully precise, then the fitted statistical model may be used to estimate the costly variables for those aquatic systems where only the inexpensive variables can be measured. Methodologically this is a case of statistical interpolation within a defined set, and not "prediction" in a temporal sense.

Recent advances using the statistical approach with lakes (Henderson et al. 1973, Ryder et al. 1974), reservoirs (Jenkins 1967), and rivers (Cuinat 1971, Welcomme 1974) show some promise for estimating baselines. All are now being used for estimating potential yield, and their extension for purposes of managing other anthropogenic stresses should not be difficult. Canadian groups working at the Universities of Guelph and Toronto are collaborating with FAO officers with responsibilities for freshwater resources in developing countries to develop this approach further, taking a variety of natural and anthropogenic stresses explicitly into account.

Of particular ecological interest is the suggestion by Lett (1975) that the classification of fish into reproductive guilds (Balon 1975, 1975a) may be specially appropriate for elucidating causal mechanisms that underlie statistical correlations. One of the basic inferences, still tentative perhaps, is that reproductive processes are more directly and strongly influenced by natural and anthropogenic factors than are trophic processes.

A third approach requires an understanding of long-term climatic, geological, geographic and related trends (see Section 3.2.5). These changes sometimes occur sufficiently rapidly that they must be taken into account in any case. We may currently be in a time of very rapid regional or global climatic changes according to Reid Bryson (1973) and others.

In a somewhat more limited way the work of paleoecologists may be useful for estimating baselines from sediment cores with preserved hard structures of animals and plants (Frey 1974). (See also Appendix 4.5.)

3.4 Broad framework for indices

Our current scientific paradigm incorporates a concept of hierarchic organization; accepts as pragmatically useful a distinction in the short term between the structure and function of parts of a system; and perceives conventional space and time to be of primary significance. In one way or another we have employed these concepts in the preceding sections. We turn to them now explicitly and suggest that together they comprise an efficient and sufficient set of dimensions for our present purposes.

3.4.1 Levels of organization

Within the hierarchic levels of organization we are primarily concerned with population, community and ecosystem levels. The fact that there are so many Linnean-Darwinian

species and that the evolutionary process is so slow rules out conventional evolutionary theory as an adequate basis for a serviceable approach, and with it goes the possibility of an exclusive emphasis on population or autecology based on such species. Proposals for a taxonomy based on functional ecological characteristics, i.e., generalized roles or niches or guilds (see Section 3.3.2.7) should be taken seriously by researchers. If by this approach the number of taxa can be reduced by a factor of, say, a thousand, then a widely relevant and practical set of indices might be developed at a functional level.

As stated earlier, the number of community types within aquatic systems might be reduced to a small manageable number by considering the primary functional role of different macrocomponents of ecosystems. In lakes and seas distinctions between the communities of benthic areas of hard and of soft substrate, and those of the pelagial volume distinguishing planktonic and nektonic components, may be sufficient. In running waters physiographic distinctions between headwaters, main stem and lower reaches and estuary are important. Some broad congruence may be noted in that headwaters resemble hard substrate communities, etc. Systems that tend to be intermediate between water and land include sudds, swamps, muskegs and marshes which resemble in some ways the soft bottom systems of standing waters. Thus we find it conceivable that a small number of communities, or semi-integrated macrocomponents of ecosystems, may be a sufficient basis for large-scale modelling.

At the ecosystem level, the classical descriptive typology distinguishes many kinds of freshwater, brackish and oceanic subsystems. Again there are far too many for our purposes.

Consider again the "strategic" proposal illustrated in Figure 3.4 (and see also Appendix 4.8). In A type systems, response properties of interest to us do not fluctuate so much that we cannot proceed on the assumption of approximate constancy of system parameters, i.e., following an adjustment to a stress the system is in dynamic equilibrium. Of course, following any marked change in stress loadings, the system will adapt; the adaptive process may be most efficiently explicated using population components, either individually or as interacting sets of populations.

In B systems, basic self-regulatory mechanisms are not seriously challenged by such external and internal factors as are acting on them. With C systems first order self-regulatory mechanisms are at least occasionally overloaded, and then major collapses and recovery sequences occur.

The shift from A to C involves a gradual change in emphasis from biotic population regulatory processes to comprehensive responses of ecosystems with respect to major exogenous abiotic and stress factors.

In summary, a minimum sufficient set of functional macro-classes at our three levels of organization might include some ten dominant guilds or functional classes, four kinds of communities and three kinds of ecosystem process-response systems. The latter may be taken as relating to three levels in an hierarchic ecological sense.

3.4.2 Space and time

The sampling and modelling problems associated with temporal and spatial variability have been sketched in previous sections.

Figure 3.4 in some general way has taken account of space and time characteristics of loadings, particularly their variability and unpredictability, and their impacts on environmental resources. This conceptualization may be sufficient for establishing major classes of response indices, and no additional time-space dimensions need be assumed at the outset.

3.4.3 Structure and function

Again referring to Figure 3.4 in class A, functional system characteristics do not vary markedly and community structural characteristics or population functional characteristics may provide the more sensitive measures of such responses as are occurring.

With set B ecosystem structure or community functional properties may be of most direct interest.

With set C major ecosystem-level dynamic processes, collapse and recovery functions, are of primary interest.

These statements should not be read as advice that only an ecosystem-level dynamic approach should be used with set C. Rather that it would appear to be most reasonable *a priori* to address set C at that level of ecological study.

3.4.4 Sufficient set

Thus we find that an ecological classification of generalized functional types and components may be useful to disaggregate the population, community and ecosystem levels for purposes of developing insights and indices of ecological response to various stresses. Further, some specialization or division of labour may be desirable, consistent with a classification of the interactions of the characteristics of stress loadings and of ecosystem properties. To repeat: for the latter purpose we propose a two-dimensional screen or ordination where the two basic variables are the expectation of the magnitude of effect and the uncertainty (temporal and/or spatial variability) of the interactive system of stress and ecological factors. Within this context important spatial, temporal, structural and functional considerations are in part accommodated implicitly.

Where a number of major anthropogenic stresses are acting on an ecosystem, and particularly if sophisticated studies and some effective regulation are already under way, the above proposals will rightly be seen as rather elementary and generalized.

3.5 Broad framework of stresses

Having dealt with scientific and ecological concepts and methodology, we turn to stress phenomena in order to analyse and classify them and then to determine in the next section whether our proposals in preceding sections are likely to prove useful and efficient.

3.5.1 Taxonomy of stresses

We suggest that the great majority of stresses on aquatic systems of ecological importance may be classified into one of the following five classes:

Natural, background as "baseline" factors;
Harvesting of renewable resources, whether opportunistic or carefully regulated;
Loading by plant nutrients, poisons, heat, or inert suspensoids;
Restructuring morphometrically by damming, shore infilling, channelization or major sedimentation;
Introduction of non-native species or biological loading.

The causal relationships underlying separate and joint effects of these major classes of stresses should be clarified to the extent that first order effects could be predicted at each of the three levels of organization - selected population, typical community, typical ecosystem.

Of the many ecological studies of aquatic systems few have examined those not already influenced to an appreciable extent by man's activities. This statement applies particularly to the "living resource" components of such systems. Many workers tacitly accept the characteristics of moderately stressed systems for purposes of establishing "natural baselines". Determining baselines in natural systems should have high priority, but existence of natural baseline estimates is seldom absolutely essential from a practical viewpoint. A proximate "standard" baseline may be adequate in many cases.

Natural factors of primary importance as influencing baseline conditions, at all three levels of aquatic systems the world over, include the average measure, the spatial or temporal variability and extreme manifestations of the following: temperature, winds, rainfall, seasonality, basin depth, plant nutrient loading, water level and currents. Taken separately and together, the effects of these natural factors at all three levels of organization are sufficiently well understood that general quantitative expressions could be estimated for broad baseline purposes with extant data (see Section 3.3.2.7). Such relationships would clearly be better than nothing and would be adequate for answering some general, first order questions. Local detailed refinement would usually be necessary.

As a broad generalization, smaller inland waters are more fully understood than large inland waters or estuaries, which in turn are now better known than the seas and oceans. This applies to all the listed natural and cultural stresses and to the three levels of ecological organization. The reasons for this phenomenon may lie primarily in the relatively low intensity of economic interest in larger systems until recently and in the comparatively high cost of relevant research.

Scale factors, together with differences in salinity and in the evolutionary effects of geological age, may invalidate a direct transfer of freshwater models to marine situations or vice versa, but we doubt that the systems are so different as to rule out broad interchange of insights, hypotheses and models.

3.5.2 Nature and intensity of loading process

Stresses may be applied to the system through a particular point as with the outfall from an industrial plant, along a broad front as with runoff from agriculture land to a lake, or quite diffusely as with aerial transport of pesticides.

Difference in loading processes may affect the usefulness of various ecological indices. In any case the sampling design and any mitigative actions are greatly influenced by such differences, thus the taxonomy of point source, broad front and diffuse should be of particular strategic interest for decision-makers.

Acute stress may occur continuously in which case the system will be largely destroyed, or periodically and then some recovery may occur between acute spells. Chronic stress is non-lethal and permits continued functioning of the system, though perhaps in some modified or crippled form.

No very sophisticated indices will be required to diagnose acute continuing stress. Death is easily recognized. It is of more interest to determine where the boundary lies between acute and chronic and between chronic and no significant practical effect. Considerations of acute vs. chronic apply across all categories proposed above and are taken to be second order considerations in our general framework.

3.6 A way of relating ecological science to users' needs

Indices may be used to monitor the state of the environment (see Section 3.1.1).

Insights on which indices are based may be used to assess the likely impact of a planned development, and indices may subsequently be applied to monitor the intensity, map the extent of the impact, and control the loading process.

Trends of index values may be interpreted in the form of a forecast or prognosis as to the likely future state of the system.

Given an observed impact of uncertain cause, sets of indices - if available and locally calibrated - may be used to diagnose the cause or causes of the effect. Diagnostic protocols have been well developed for a variety of systems (e.g., physiological, mechanical, business), but are still at a primitive state for most ecological systems.

3.6.1 Symptoms, syndromes and diagnosis

The response of a system to a stimulus or stress as measured by the deviation of a particular variable from normal may be termed a symptom. The set of all such symptoms may be termed a syndrome.

If a number of kinds of stresses evoke responses that - at the appropriate level of organization - are similar with respect to numerous variables, then a large overlap of separate syndromes occurs. A generalized response of this kind to "stress" broadly defined has been termed a general adaptation syndrome or GAS (Selye 1974).

Clearly if the intention is to develop diagnostic indices for different kinds of stresses, then those symptoms which are commonly present in the GAS set are unlikely to prove very useful. Instead they may serve well the purposes of specifying the general state of the system since the GAS set will reflect an integration of responses to the various separate stress insults.

An analysis of fish communities from this viewpoint has led to the suggestion (Regier and Henderson 1973, Regier and Loftus 1972, Regier 1973) that a common response of fish communities to increases in the stress factors listed above - except perhaps to biological loading - is a general shift in the direction of relatively more smaller, short-lived pelagic fish species. Decreases in the factors should work to the relative advantage of benthic forms. A simple index might consist of the ratio of pelagic fish biomass to benthic fish biomass.

A shift to smaller organisms is an adaptation or response to severe loading stresses noted with other kinds of organisms and ecosystems (Kerr 1974). But we do not wish to imply that it is a fully general response to all severe stresses.

We emphasize that though a particular variable defined at the community level may respond similarly to different stresses, we do not suggest that the causality mechanisms are similar. In fact, in the case of fish noted above, the mechanisms appear to be quite different. Indices diagnostic of the separate causes might well be deduced from an understanding of these different mechanisms in that they must involve different variables or the same variables quite differently.

The general adaptation syndrome tentatively sketched above should be carefully distinguished from an ad hoc numerical combination of a number of quantitative measures. This approach has become popular particularly in the U.S.A. with air pollution monitoring and occasionally with aquatic pollution. (It is analogous to some of the indices used to measure activity in stock exchanges.) On the basis of some partial understanding of those stress variables that are known to be associated with certain undesirable ecological or human responses, a single weighted average of stress variable readings is assembled and then calibrated statistically against responses that have occurred at different levels of the average index. Though admittedly better than no data at all, the approach is scientifically primitive and crude (see Appendix 4.6).

In the long term the most effective and efficient system of indices will contain those developed from a comprehensive and intensive understanding of the causal mechanisms that relate response type to the stimulus type.

3.6.2 Diagnostic keys

Most and perhaps all scientists are familiar with the use of diagnostic, taxonomic or classificatory keys or protocols. Biological systematists key out the identity of species, chemists of compounds and elements, physicists of elementary particles, physicians of physiological or physical abnormalities, geographers of land forms, etc. In our intended application of structural indices we approach keys using visible properties in the manner

of systematists and geographers, while with process or functional indices we resemble the chemists, and physicists and physiologists in that we employ variables not commonly perceived by the layman.

Some desirable attributes include the following:

- The attributes can be expressed in clearly contrasting forms, and ideally in binary (yes-no) form;

- They should be easily measurable and obvious rather than obscure;

- They should be comprehensive for the set addressed, which in turn is clearly and explicitly bounded;

- Non-quantifiable, non-unique, or infrequent symptoms should be listed for separate stress factors to provide additional checks following an apparently successful passage through the key.

The first dichotomy in a key inevitably assigns a heavy weighting upon the attribute chosen for this purpose. This weight carries its bias into human thinking and tends to "fossilize" a key.

In classificatory jargon, keys involve divisive classification (breaking from the top downwards) and may be monothetic (using only one attribute at a time). Several computer techniques very effectively handle data in this way. The approach has been termed "old fashioned" by some proponents (Sneath and Sokal 1973) of the alternative agglomerative classification (builds from bottom upwards) and is polythetic (uses many attributes throughout). Both approaches might be applied in the present context.

3.6.3 A users' framework

It is consistent with our considerations and analyses above that for each of the four community types (hard and soft bottom benthic, planktonic and nektonic pelagic) and for each of acute and chronic classes, three broader dimensions are of most general and primary interest for our practical purposes:

(i) Five types of stresses - natural, exploitive, material loading, morphometric restructuring, and biological loading.

(ii) Three kinds of loading mechanisms - point source, broad front, diffuse.

(iii) Three classes of the expectation x uncertainty ordination, simply put - low uncertainty, moderate uncertainty, high uncertainty.

To some extent - certainly not fully - these three "dimensions" internalize some aspects of the "dimensions" specifying three levels of ecological organization, a spatial pattern parameter, a time series parameter, and a physical scale parameter (see Section 3.4.4).

To the extent that these latter dimensions are not already accommodated, they may be taken as aspects of secondary significance to be dealt with explicitly as the occasion warrants.

The insights of the various schools of ecology are the bases from which appropriate indices are developed to be nested within the basic three-dimensional or extended seven-dimensional framework.

Appropriate classificatory, statistical, computational and logistic methods have been sketched and have all now reached a level of sophistication so that they do not pose

serious difficulties. These may also be nested within each of the cells of the basic practical matrix.

3.6.4 State of the art

For each of the five stress classes separately, we present examples of stress phenomena for each of three expectation-uncertainty classes compounded by each of three kinds of loading regime (see Table 3.3). This amounts to a 5 x 3 x 3 three-dimensional matrix. For each cell we indicate our subjective judgement on the state of availability of indices and relevant methods. Thus one asterisk implies that the level of understanding is quite low and few if any useful indices have been proposed or tested. Two asterisks imply a moderately comprehensive understanding with some indices already in use. Three asterisks imply a level of development adequate for many normal purposes.

We advise against any immediate or facile attempt to apply these summaries directly into practice. Our work is an attempt by ecologists to find a framework within which users may be able to relate ecological science and the methods of various schools and perspectives to users' particular needs. The approach is at an early stage of development; an alternative more useful proposal may soon be made by other workers unknown to us.

Table 3.3 Examples of various stresses classified by type of loading regime and expectation-uncertainty classes

Response: Expectation-uncertainty class	Types of stress loading: Continuous point source	Broad front	Diffuse in time and space
(a) Natural or baseline stresses			
Moderate to high values, low uncertainty	**large river into sea	*water mass boundary shifts	**seasonal weather patterns
Low to high values, moderate uncertainty	**annual floods on flood plains	**upwelling, coastal land-water interface	*epizootic mortality outbreaks
Low to high values, high uncertainty	*volcanic eruption	*tsunamis, storm surge tidal wave	*forest fire, ashes and erosion; red tide

Response: Expectation-uncertainty class	Type of stress1/: Highly selective, closely regulated in restricted area	Broad range, opportunistic, ubiquitous	Intermittent, areally spotty pulse fishing
(b) Renewable resource harvesting stresses			
Moderate to high values, low uncertainty	***Pacific halibut before 1954	**Northwest Atlantic before 1960	unknown
Low to high values, moderate uncertainty	***Bodensee Blaufelchen; Oncorhynchus	***Lake Erie before 1945; reservoirs	*Northwest Atlantic since 1960
Low to high values, high uncertainty	**Peruvian anchoveta since 1973	*Kafue Flats flood plain	*Great lakes clupeids

1/ Note that the specification of types of stress is different with harvesting than with natural, etc. Rather than use some very general wording, we have used more specific terms that are approximately analogous across the five types of stresses.

Response: Expectation-uncertainty class	Types of stress loading		
	Continuous point source	Broad front	Diffuse in time and space
(c) Loading by plant nutrients, poisons, heat or inert suspensions: a perspective applicable to the Baltic region			
Moderate to high values, low uncertainty	***Domestic sewage outlet	*Chlorinated hydrocarbons in precipitation	*Trawling, dredging of the seabed
Low to high values, moderate uncertainty	***Papermill wastes	**Acidification of lakes from smoke	*Land runoff from agriculture
Low to high values, high uncertainty	**Chemical industry's sewage	**Oil tanker spills	**Fallout from nuclear weapons
(d) Morphological restructuring: "uncertainty" here refers not only to predicted events following the impacts, but more particularly to ecologists' guesses of what decision-makers will actually decide to do during the planning process			
Moderate to high values, low uncertainty	**River alteration below dams with controlled discharge	**Shoreline alteration by cottage development	*Reservoir filling resulting from land denudation
Low to high values, moderate uncertainty	**Low dams or main reservoirs (Jebel Aulia, Kafue)	*Landfill for urban housing development	*Seabed mining formation
Low to high values, high uncertainty	*Siting electric power installations, high dams or storage reservoirs1/	*Construction of causeways across water bodies	*Water filled bomb craters (south east Asia)
(e) Biological loading			
Moderate to high values, low uncertainty	*Introduction of Pacific salmon to Baltic, *Elminius modestus*, a barnacle, into Europe	*Spread of whirling disease of trout in Canada	**Stocking of hatchery raised native species, *S. mansoni* in America
Low to high values, moderate uncertainty	*Canals as migratory bridges (Welland, Suez, Panama Canals)	*Spread of *Orconectes propinquius* in north central U.S.A. by fishermen	*Stocking of grass carp in U.S.A.
Low to high values, high uncertainty	*Unknown	**Human waste-borne disease; **Bufo marinus* in Australia	Cholera epidemics

1/ The loading is not usually seen as continuous. Once the system comes to a new equilibrium it is no longer considered as "stressed".

4. TECHNICAL APPENDIXES

4.1 Searching for groupings in species in space and time

Biological sampling at the species level rapidly produces masses of data. In complex situations it is difficult to derive conceptual sense from the array. There are two complementary approaches toward simplification. The first uses multivariate methods of analyses, e.g., Cassie and Michael (1968). They involve such things as principle component analysis, principle coordinate analysis and factor analysis. Clifford and Stephenson (1975) should be consulted for explanations and critical evaluation, and the partial bibliography for additional references.

The second approach toward simplification is by classification and this we now elaborate. If we can find groupings within the data pictures may emerge, and one way of detecting the presence of a stress in a system may be to look for shifts in these groupings.

We now consider the techniques of revealing groups, assuming that biotic data have been obtained on species (s) in sites or quadrats (q) in times (t). Clearly these give a three-dimensional matrix of s x q x t. Methods of handling such matrices have been explored by Williams and Stephenson (1973), by Stephenson, Williams and Cook (1974), and by Stephenson, Raphael and Cook (1976 in press). Methods are still evolving (Stephenson, personal communication). In the above work, data are meristic (i.e., whole number) counts of individuals, but the techniques are readily applicable to graded or ranked or binary (i.e., presence/absence) data.

A number of options are available. The first possibility is to evaluate the relative importance of space and time. If data are complete an analysis of variance method using transformed data may be appropriate, but there are other alternatives.

Following this the procedure has been to "collapse" the original three-dimensional matrix into three separate two-dimensional matrices. By summation over species we derive a q x t matrix, which in its original form evaluates population changes from place to place and from time to time (N values). Alternative q x t matrices are readily derived, for example the number of species (s values) in each sample, and any of several diversity measures per sample or per individual per sample.

An alternative summation over times gives an s x q matrix of species by sites. These can be classified by one of a number of numerical methods (see Clifford and Stephenson 1975) and produce site-groups characterized by the species present together with species-groups characterized by their sites of occurrence. (The "reality" of such groupings can be confirmed by tests of significance whose use is still being explored. See also Knight and Tyler 1973.)

The above analyses permit description of "communities" approximately in the sense of Peterson (1914) as areas characterized by species and approximately in the sense of Fager and McGowan (1963) as groups of species characterising given areas. Because they involve summation over time they give an "average" picture. (It should be noted that the Fager type groupings use only binary data and concern only species groups.)

Comparison of such pictures before and after stress gives important insights into the magnitude and extent of the changes. This has been demonstrated by studies of the effects of a devastating 100-year flood on the benthic biota near the mouth of the Brisbane River (Stephenson, personal communication). It also gives information on the foci of recovery in terms of area and species.

The third alternative summation is over sites and gives an s x t matrix of species by times. Again times-groups and species-groups can be derived by classification and are analogues to the "community" groupings previously derived. Using one set of data, further analyses showed that time could be treated as two-dimensional with distinction between

seasonal and annual effects. Eventually we derive species-groups characterising sites and species-groups characterising years (Stephenson, Williams and Cook 1974). This has implications for the diversity school (Clifford and Stephenson 1975) and for community concepts generally (Stephenson 1973a).

In recent work (Stephenson, Raphael and Cook 1976), interactions in time and space, and at the specific level, have been explored. This indicated the areas where the more pronounced temporal changes were occurring, and thus spatial differences in baseline fluctuations. In current work (Stephenson, personal communication) this approach has revealed differences in the effects of a natural catastrophe from place to place.

4.2 Growth parameters in analytic models

The parameters in mathematical growth models of individual species may sometimes be used as indicators of the condition of the community or ecosyst‹

Mathematical equations in population biology are often empirical models which use least-squares criteria to compress data into a concise symbolic form such that y-values are some function of x-values. In contrast, there are analytic models which are equations whose variables and parameters are, *a priori*, designated as representing those specific biological processes thought to exert primary control over the phenomena under study. Systems models often result from combining (and complicating) several analytic models with the result that closed-form analytic solutions are replaced by "number-crunching" solutions.

The analytic model discussed here is the von Bertalanffy growth model which has parameters of interest K, the growth rate and L_∞, the maximum size an animal may assume. Of course the principles suggested below are applicable to any analytic model, and this is not an endorsement of any one model for all circumstances.

Most studies terminate upon fitting the model to the data and testing the model's predicted values against the observed data. It is suggested that these steps be preliminary to using the model's parameters to test if a population is stressed by a comparison to parameter values estimated before the stress occurs or by comparison to another population's parameters (Gallucci, personal communication).

If the population is in a steady state it may be sampled to determine a size-at-age curve (Southward and Chapman 1965). In the case of the von Bertalanffy model, K and L_∞ are estimated by standard regression methods (Beverton and Holt 1957). Since the data are drawn from the whole population, K and L_∞ are population indices.

The remaining step is the statistical comparison of indices K and L_∞ to K' and L'_∞ corresponding to indices from the stressed and unstressed populations, respectively. A chi-square test (Rao 1973, pp. 389-391) is suitable. Formally, the compound null hypothesis is $K = K'$ and $L_\infty = L'_\infty$.

The advantages of this coarse approach to detecting change are: models may be chosen which are often well known to biologists, the parameters or indices are statistically estimated from the population and the indices may be statistically compared for differences. The outstanding feature is, however, that changes in indices have been calibrated with the critical biological processes taking place. Furthermore, for specific animals, changes in some parameters will be indicative of specific ecosystem changes (Gallucci, personal communication, Lewis and Bowman 1975). That is, effect may be specifically associated with cause.

4.3 Recruitment-related indices

Experimental studies on the effects of pollutants and other anthropogenic stresses on aquatic organisms are pointing toward the higher susceptibility of the reproductive processes and stages compared with that of the post-recruitment phases (Boney 1970, Connor 1972,

Table 4.1 Primary and secondary effects on river benthos of three levels of loading by biodegradable organic material (from Wuhrmann 1974)

	Primary, defining effects	Secondary (not defining) effects (main determining ecological factors: hydraulic conditions and temperature)
Heavy organic pollution (polysaprobic)	Microphytic biomass almost 100% heterotrophic (bacteria fungi, flagellates), aerobic and/or anaerobic; phototrophic microphytes may be ± present, ecologically unimportant	Autrophic anaerobes and microaerophilic microphytes frequent, protozoic fauna rich (anaerobic and aerobic), metazoic fauna dominated by forms requiring only low oxygen tensions irrespective of flow conditions (or air breathers)
Recognisable, though moderate, organic pollution (mesosaprobic)	Microphytic biomass of phototrophs and heterotrophs in variable proportion, phototrophs in aspect and biomass always strongly dominating	Anaerobiosis only in slow current biotopes, sediments and subrheal space; mostly rich, aerobic protozoic fauna; diversity of metazoic forms strongly dependent on hydraulic conditions, wide spectrum of ecotypes
No organic or very slight pollution (oligosaprobic)	Microphytic biomass strictly phototrophic; heterotrophs only microscopically, on a weight basis in negligible amounts	Anaerobiosis only as exception in small biotopes, sediments and subrheal space essentially aerobic; spectrum of metazoic forms as above, including the most exacting species in respect to oxygen requirements in any stage of development

Table 4.2 Predicted effect of increasing water temperature on the fish community of the Columbia River[1/] (Bush *et al.* 1974)

°C	% of species within preferred temp. range	% of species in suboptimal temperature conditions[2/]	% of species expected to be lost from the system	Species expected to be lost from the system
8	100	0	0	
10	95	5	0	
12	93	7	0	
14	88	12	0	
16	60	40	0	
18	54	44	2	Columbia River smelt
20	51	44	5	Freshwater smelt
22	28	65	7	Puget Sound smelt
24	26	48	26	Sockeye salmon, chinook salmon, chum salmon, pink salmon, coho salmon, Dolly Varden, Rocky Mt. whitefish, chiselmouth jack
26	16	44	40	Brook trout, Aleutian sculpin, prickly sculpin, Columbia sculpin, sculpin, starry flounder
28	9	49	42	Lake trout
30	9	26	65	White sturgeon, green sturgeon, American shad, cutthroat trout, brown trout, longnose sucker, tuichub, squawfish
32	7	12	81	Rainbow trout, coarsescale sucker, yellow perch, freshwater burbot, Columbia finescale sucker, chiselmouth, longnose dace, western speckled dace, Columbia R. chub
34	0	14	86	Redside shiner, threespine stickleback
36	0	7	93	Tadpole madtom, smallmouth bass, black crappie
38	0	0	100	Carp, largemouth bass, bluegill

1/ Based on preferred and lethal temperature data for adult and juvenile fish. Where specific data for a species were unavailable, data from closely related species were used.

2/ The temperature range above the preferred temperature and below the lethal temperature.

Davis 1972, Katz 1973, Mironov 1972). This suggests that indices relating to levels of reproductive activity in the field or to the zero age classes of populations would be worth developing.

These same processes extending between germ layer development and recruitment into field populations may however be very sensitive also to a number of natural abiotic variables (Mileikovsky 1974, Thorson 1966). Striking correlations have been observed particularly between reproductive success or failure and anomalies of climate in, for example, oysters (Korringa 1957, Quayle 1964), other bivalves (Sastry 1966, Quayle 1964, Stephen 1938), limpets (Lewis, personal communication), and fish (Christie and Regier 1973, Balon 1975). In addition to these specific cases we may note the more general occurrence of seasonality of breeding in temperate latitudes, and the intermittent or regular lack of breeding that occurs toward the limits of geographical distribution. From such observations it would appear that indices of gonad condition or field recruitment could be the most sensitive indicators of field response during the life span to a spectrum of climatic stimuli that are related to and perhaps most easily measured by temperature. Being concerned with the crucial matter of population maintenance, they would clearly bear upon a highly important baseline aspect.

Although reproduction/recruitment are responses at the species level, the varying success from year to year of each individual species within a community will clearly influence many attributes of the community as a whole. There is a reasonable generalisation, which may not apply without exception, that the extent of this influence will be in broadly inverse relationship to the life spans and number of generations present.

Among some benthic communities the impact of annual fluctuations in individual species is further intensified by their 'key-species' structure and the spatial competitive controls that exist (see Section 3.2.5). Furthermore, there are increasing examples in these communities that even when the first phases of reproduction have occurred, ultimate success may go to the species that happens to be breeding when space becomes available. Such species may successfully exclude other potential users of the same space, but they may also provide a substratum for a large number of dependent species (Lewis and Bowman 1975, Dayton _et al._ 1974, Lewis 1970, Gallucci, personal communication).

The practical value of such indices would be vitiated if their sensitivity to natural abiotic stimuli were very high, for a confusingly wide spectrum of background noise would exist. This point can only be resolved by long-term practical experience that has yet to be underwritten. Should such indices become useful interpretative tools they would be of particular value in predicting the responses to natural abiotics and thereby facilitating detection of the responses to other stresses. Furthermore, the record of past reproductive success that is contained in some, but not all, age/structure data of population samples permits retrospective monitoring to take place. Finally, their availability and reliability might well decide the particular populations or communities selected for monitoring purposes.

4.4 Indicators, elimination and recovery sequences

Indicator species have been used for many decades to monitor types and levels of a variety of pollution stresses. _Either_ the presence in abundance of particular species not to be expected in the area under natural conditions, _or_ the absence of species to be expected there, provides information. European limnologists have long debated the "saprobic system" (Sládeček 1973). Wuhrmann (1974) states: "No other subject has either consumed so much paper in applied limnology or has provoked such heated discussions". Table 4.1 from Wuhrmann (1974) is a generalised condensation relating the composition of the benthos of rivers subject to loading by degradable organic compounds.

Mar _et al._ (1973) have designated as "ecological accounting" an approach conceptually not far removed from that of indicator species. Using laboratory data on thermal requirements of eightyfive species of freshwater fish summarized by Bush _et al._ (1974), they predicted the effect on the extant fish community (or "fish taxocene") of elevated water temperature. Table 4.2 is their example for the Columbia River in U.S.A. (Bush _et al._ 1974).

Harvey (personal communication) has developed an analogous series for effect of elevated acidity (decreased pH) on the set of oligotrophic Killarney Lakes in Ontario (Figure 4.1). These data were obtained by sampling lakes of different acidity due to atmospheric loading of sulphur dioxide, in some cases during years when acidity was increased rapidly. Data in Figure 4.1 are in preliminary state and no high precision should be inferred for the data on species that are not commonly found in these lakes. These data, again, apply to a set of lakes and the fish of each lake will not necessarily respond in precisely the way indicated by the average over the set.

Much good work has been done on the effects of toxic ions and substances as influenced by a variety of limnological variables, particularly at the Stevenage Laboratory in the U.K. (Alabaster et al. 1972, Anon 1974) and in various laboratories of the U.S. Environmental Protection Agency.

The foregoing examples and citations relate to stresses due to loading by biodegradable organics, heat, acid and toxic materials. Our impression is that, of the vast amount of this kind of information already available, relatively little has been assembled, mobilised and transferred into effective practice.

4.5 Retrospective modelling

Any species is an integrator of its environment but in some species the time record is preserved in a relatively easy-to-read form. The interdisciplinary literature of paleo-ecology contains references to many populations and communities which are suitable for establishing a historical record of the environment. As with any integrator or index, detail is lost in favour of a gross measure.

Extensive retrospective analyses have been done using tree rings and a major dendro-chronology centre has been established by the University of Arizona. The methods of time series, spectral theory and multivariate regression are commonly used (Fritts et al. 1974). The work provided a perspective for evaluating contemporary stresses such as forest fires, insect epidemics and climatic anomalies.

The aquatic environment contains a clear analogy in the hard parts of certain mollusc shells and corals, as well as fish scales and otoliths, in the sense that annual rings of certain widths are often preserved. These have meaning in terms of animal age and limiting factors such as space, temperature, food available, etc., and thus are crude indicators of climatic condition.

Furthermore, by the use of old mollusc shells from a sample of the population one may infer rates of growth, age distributions and information about catastrophes. Fundamentally, the technique consists of inferring information from the pattern of the relative frequency of occurrence of size classes.

A living community in which breeding takes place during a relatively short period at the same time each year has a size-frequency distribution which is multimodal. Communities of this type are typical of temperature and boreal seas. Communities consisting of organisms with preservable hard parts (such as bivalves) give rise to fossil communities with size-frequency distribution of a characteristic form. For example, (a) by catastrophic death, the size-frequency distribution of the living community is changed directly into the distribution of the fossil community. A community which suffered catastrophic death is shown in Figure 4.2 where yearly recruitment to the living community is preserved in the fossil community; (b) if high mortality occurs periodically during a short period of time across all ages at the same time each year, then the fossil community also shows this. A community which may have been formed in this way is shown in Figure 4.3. In similar ways events such as selective mortality or unusually heavy predation may be detected (Sheldon 1965, Hallam 1967).

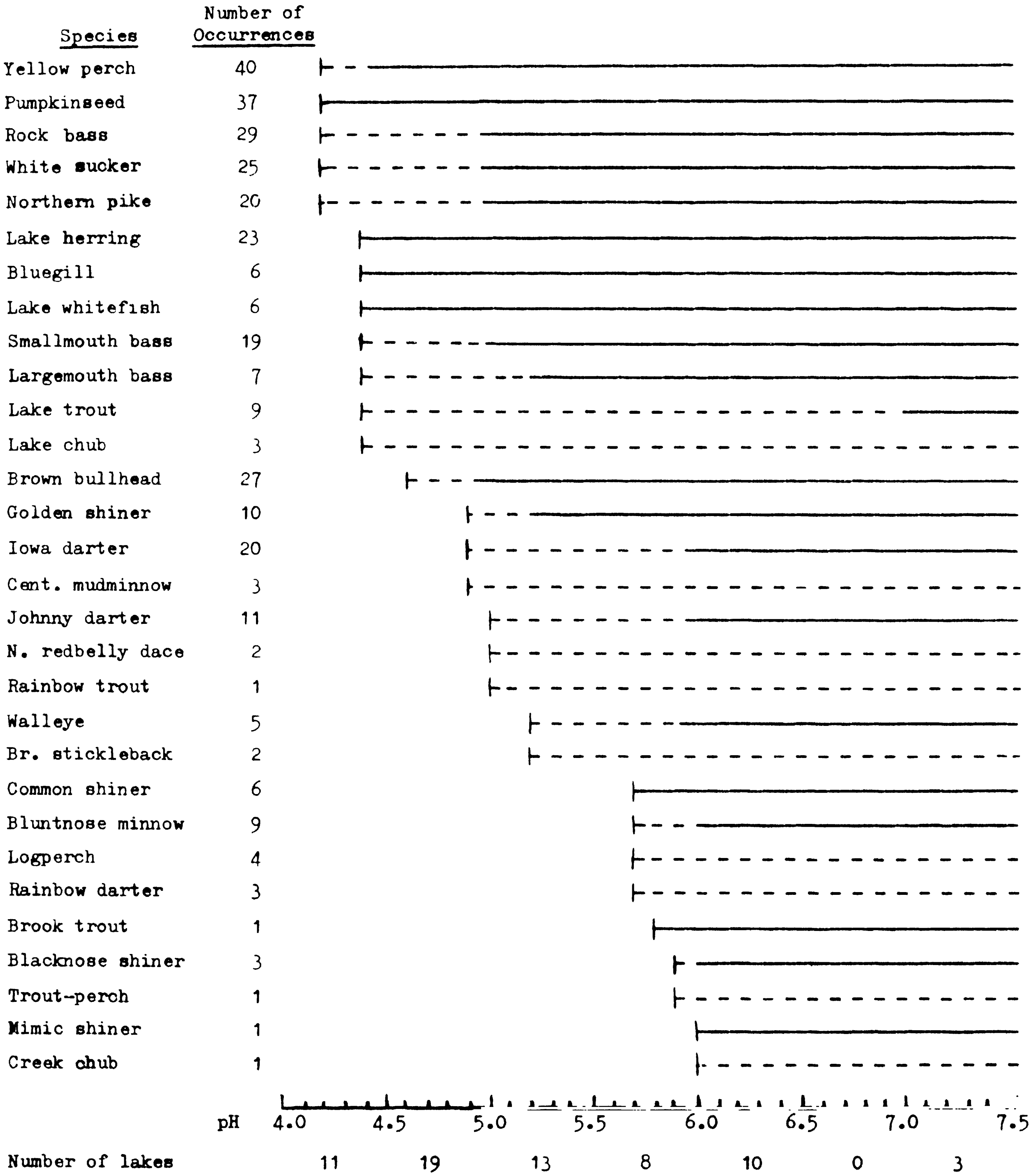

Figure 4.1 Empirical field data on the incidence of species of fish in the Killarney Lakes of Ontario, Canada as a function of acidity or pH. A continuous line indicates the range within which no serious reproductive and recruitment impairment was observed. The dashed line denotes highly variable recruitment from year to year, with some unknown part of the failure ascribable to acidity. The vertical blip at the left end of the line denotes the observed limit of acidity at which the particular species was found to be present in the lake. (From Harvey, personal communication.)

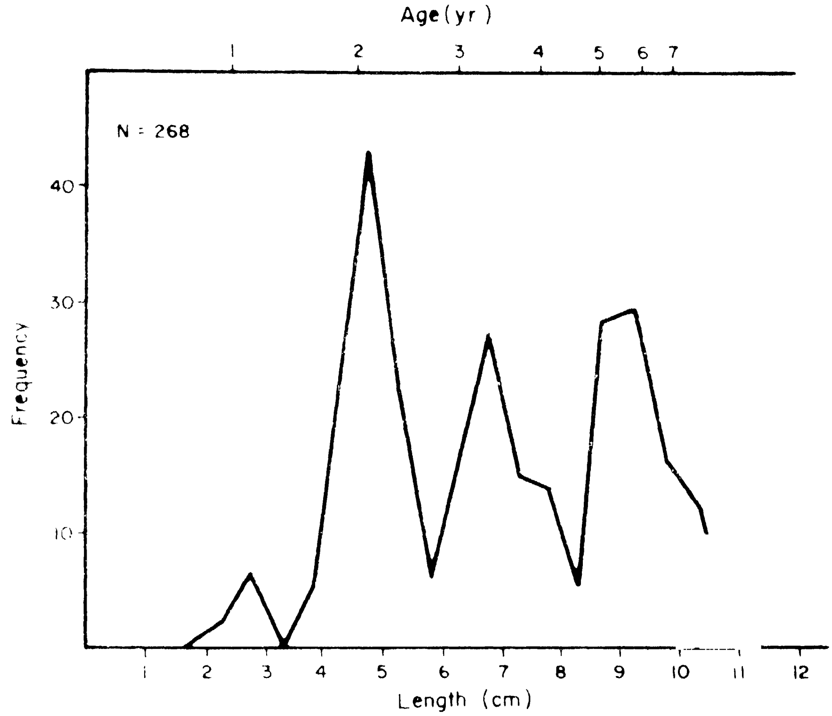

Figure 4.2 Size frequency distribution when a catastrophic death occurs. (Sheldon, 1965, from Nature, used with permission)

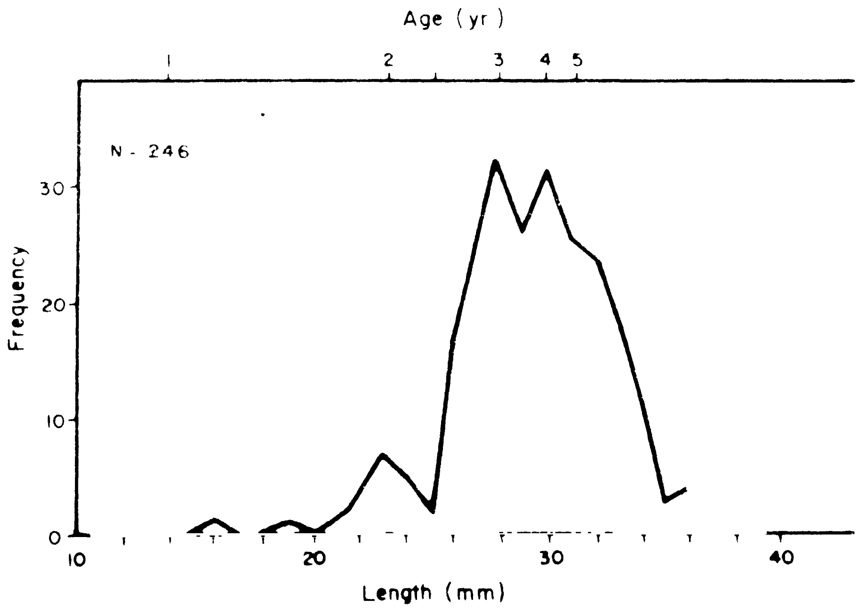

Figure 4.3 Size frequency distribution when death occurs periodically. (Sheldon, 1965, from Nature, used with permission)

The use of core samples in which stratification has occurred also permits extrapolation backwards in time. The contents of strata: zooplankton tests, half lives of various chemical elements in the strata, pollen, invertebrate spines, etc., all contribute to a crude picture of that year (Webb and Bryson 1972, Frey 1974).

Thus, retrospective techniques provide information which can be invaluable to the decision-maker who must try to put into perspective the contemporary event. Such analyses were contributions to decisions made over Acanthaster (Crown of Thorns) and DDT spraying of Tussock Moth.

Agglomerate indices of environmental quality[1]

For areas or regions affected by a multiplicity of stresses it has become tempting and almost fashionable to construct agglomerate indices of environmental quality. Environmental quality is inferred from the index of contaminants present when each component is "scaled" to convert it into common units and "weighted" to reflect its relative (ecological) importance. If this approach is to be useful, we must have sufficient knowledge of the often complex synergistic and antagonistic effects of multiple stressors acting simultaneously on a given environment.

In the case of ionizing radiation, sufficient information exists on the relationship of dosage of various sorts of radiation (alpha, beta, gamma, neutron, etc.) and human health to enable the construction of a reasonable index of the hazard of exposure to radiation.

Unfortunately, in many situations in which agglomerate indices have been constructed (air pollution, water pollution, land pollution), so little is presently known about the synergistic effects of the multiplicity of environmental contaminants that such indices would appear to be premature. In practice, the demand for simple, comprehensible index numbers, regardless of their tenuous interpretation, has led to the widespread use of agglomerate indices. To cite one example of the folly of this procedure at the present time, we refer the reader to Table 3 of the Final Report on Planning for Environmental Indices (NAS/NAE). This table provides data on three different indices of urban air pollution calculated for ten U.S. cities for the 1968-70 period. A comparison of the values of the three indices reveals that the indices do not agree as to the "best" or "worst" air pollution years for five of the ten cities, and show wide discrepancies in the magnitude of change over the period in other cases. These discrepancies would appear to arise from both lack of agreement as to what to include in the index and how the components should be combined. Often, in the absence of knowledge of the synergistic effects and biological effects of each component, the separate components of air quality indices are given weights of 1. This procedure is not an acceptable alternative to adequate knowledge of the stressor-response system.

While advances in our understanding of the relationship of air contaminants to human health might eventually provide a basis for the construction of air pollution indices, there are other types of agglomerate indices for which no such prospect is in sight. Take, for example, the proposal for a national environmental quality index for Canada (Inhaber 1974). This index lumps together data on various aspects of the environment such as air quality, water quality, land quality, aesthetic considerations, accessibility of parklands, etc. The result is a single index number which is purportedly a guide to changes in the Canadian environmental quality. This approach suffers not only from the lack of knowledge about stimulus-stress-response systems as already discussed with regard to air quality indices (only one of the many components of Inhaber's National Index of Environmental Quality), but also from a lack of a logical methodology by which one can meaningfully combine information about such diverse aspects of our total environment.

1/ Our thanks to Dr. D.J. Rapport for this section

Solving the problems of scale by converting each separate factor into a dimensionless index number does not solve the problem of assigning weights to each component. The weights that were used in this case were "subjective" weights reflecting the relative importance of each element of the environment to the individual (or group) assigning such weights. However, "subjective" weights are an inadequate proxy for the complex ways in which the components of our total environment contribute to our individual and collective environmental quality. (Clearly one man's food is another man's poison.) Economists have attempted an analogous, and in principle much simpler task; namely to find a societal preference function for economic goods. This has never been successfully resolved, even on theoretical grounds (in part due to problems of interpersonal utility comparisons), and it appears unlikely that this approach will be any more successful in the far more complex area of man's total environment.

4.7 An abstract view of resilience and stability[1/]

Ecological systems change over time as a result of natural processes (succession, evolution) or man-made perturbations. In describing how a complex dynamical system responds to stress, topological models of the type developed by the French mathematician René Thom may be useful (Thom 1970). In Thom's view, complex dynamical systems are described by flows or trajectories on a topological space or global form which is constructed from the local properties of the system. Thus a conceptual picture of changes in complex dynamical systems emerges which is useful when the system is capable of undergoing radical transformations from one stability domain to another. Holling's computer simulations of population interactions (Holling 1973) suggest that "catastrophes", Thom's term for singularities, are a characteristic of ecological systems.

Using a somewhat different mathematical approach Holling characterizes dynamical ecological systems in terms of two fundamental properties: resilience and stability. Holling defines resilience as a property of ecological systems which determines the persistence of interrelationships within the system, and measures the ability of these systems to absorb changes-in-state variables and still persist. Thus "resilience is the property of the system, and persistence or the probability of the extinction of a state is the result". Holling associates stability with the manner in which the system returns to a steady state after a temporary disturbance. If an ecological system is sufficiently perturbed (a "catastrophe") simulations indicate that the system may change to a new steady state, which may be considered as a qualitatively different ecosystem.

These conceptualizations suggest the following for the use of new indices of ecological stress-response systems:

(1) A search to find indicators of the stability and resilience properties of the system and the subsequent monitoring of these attributes of the system over time.

(2) When the system is subjected to sufficiently large perturbations rapid transformation system responses may be anticipated.

(3) Finally, topological thinking conceptually underscores the possibilities of irreversibility in ecological systems and may enable one to anticipate irreversible responses.

4.8 A mean-variance context generalized

Both the mean and variance of a variable - say of a yield output of a natural resource system - have long been of interest to decision-makers. Extrapolated or projected into the future they measure the expectation, and the uncertainty to be associated with the expectation.

1/ Our thanks to Dr. D.J. Rapport for this section

Quite a number of somewhat different scientific schools or traditions have developed in fisheries. An attempt to classify these within a large-scale mean-variance context led to a two-by-two table in which both mean and variance were divided into small and large components (Regier 1974, Regier et al. 1974). An alternative though roughly analogous approach was attempted following a suggestion of Beverton (1974) that continuous scales be used for the two variables (see Figure 4.4).

This classification of fishery work and workers can also be considered as an overlay upon a classification of fishery problems, which themselves are largely bound by the mean-variance characteristics of the unit fishery resources addressed. In the figure, this mapping of workers upon resources leads to a horizontal scale, expectation of a unit resource, extending from less than 10 kg/year of bass from a small managed pond to about 10^{10} kg/year of anchoveta in the upwelling system off Peru. The uncertainty, as standard deviation of annual catch, or equivalently, the confidence interval that can be placed on the catch, say five years from now, has a similar range of about ten orders of magnitude.

The utility of the mean-variance contrasts seems quite general and is readily extended to other uses of aquatic systems in addition to fisheries. We may expect different perspectives, different decisions, and different actions in response to accidental discharge of a drum of oil in a small pond than to the discharge of the contents of a super tanker in a coastal area.

Along the lowermost edge of the general mean-variance or expectation-uncertainty space, rather simple formulations of goals and decision rules are possible. Scientific models may be made deterministic and quite precise. A useful approximation to optimization of output may be possible. On the upper side of the space, however, decision rules must be based on a variety of contingencies which in many cases can only be usefully modelled on an actuarial basis if at all. The primary concern of the resource user, entrepreneur or decision-maker will be with the contrast between potential gain and possible loss of any investments. The harvesting and/or management strategies of the resource users are likely to be based on averaging good and lean years. If the uncertainty includes the possibility of bankruptcy, or for other kinds of users loss of life, a minimax decision rule may apply. Under minimax the first consideration is to minimize the risks of the maximum loss, rather than, say, to maximize the yield itself. To the extent that the uncertainties can be modelled actuarially and the risks quantified, optimization procedures may be extended to such resources. But a certain increased cost would need to be charged to the increased social and institutional flexibility and redundancy that would be required. Aspects of these questions have been examined by Bella and Overton (1972), Bella (1974) and Watt (1974).

On the right hand edge of the space the unit resources are vast permitting specialization not only of individual users or harvesters, but also of vertically integrated, capital-intensive industries. Large communities may depend on such unit resources, and large corporations - both private and state - evolve to dominate such systems. These large, vertically integrated giants participate in the "planning system" (Galbraith 1973) and can assign profits to different components of their enterprise simply by internal accounting devices. Such industries can interfere with and eventually cripple small entrepreneurs by well hidden mechanisms.

It is clear, at the right side, that issues of sustained yield or wise management are complicated greatly by questions of who incurs costs and who receives benefits. It is with respect to such systems that the great weaknesses in the common property-free access-willing consent regimes have become well understood. International commissions and conventions have dealt - albeit ineffectively by and large - with these kinds of resources in the first instance.

On the left side, where unit resources are small, either absolutely or as discrete components scattered within a mosaic of other resource types, harvesting enterprises commonly spread their activities over a number of resource types. Such enterprises tend to be small, labour-intensive, with a large component of husbandry and cultural practices to enhance the yield of the more desirable resources. Ultimately domestication may be involved.

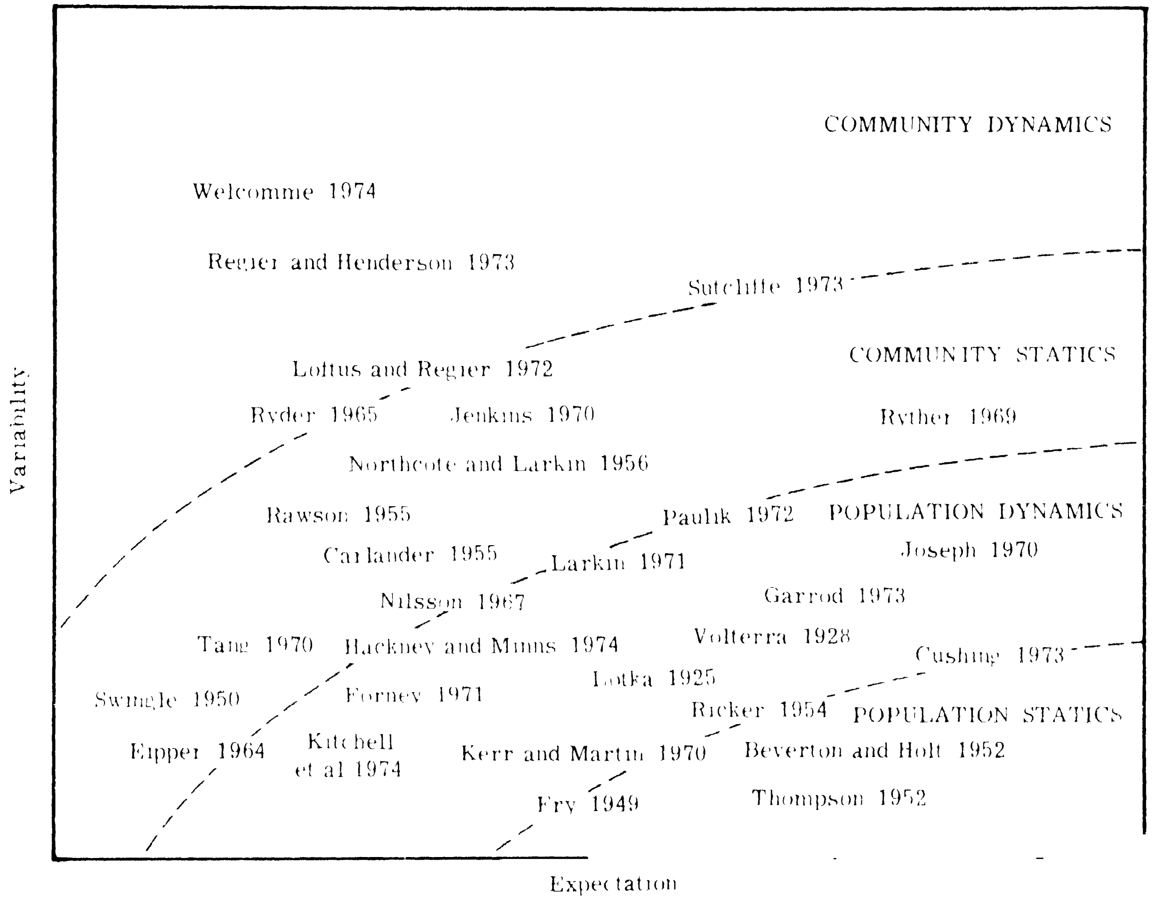

Figure 4.4 Classification of fishery workers and problems in relation to expectation of yield and variability of yield. The most appropriate level of ecological organization to be addressed directly in research and management of a fishery resource depends on the average catch or expectation and the predictive uncertainty or variability of the individual unit stock or stocks comprising the resource. Both axes are logarithmic and extend over some 10 orders of magnitude, up to 10^{10}kg/yr. Each of the four alternatives, here sketched for ecological science, has roughly congruent counterparts in economics and sociology. Different kinds of decision-making rules and mechanisms have evolved for different parts within this expectation X variability domain. Unless special precautions are taken, fisheries and other stresses singly or jointly tend to destabilize the resource ecologically and "drive" the resource system upwards in that domain. Eventually an interdisciplinary approach, that was originally quite adequate, may be rendered obsolete through such destabilization.

Enterprises within small, mixed resource systems usually are accorded a large measure of property ownership or rights, but are subject to the forces of the market place. If that market place can be strongly influenced by large interprises elsewhere, marketing cooperatives and marketing boards may be established to develop adequate power to balance that of the large corporations. These tend to become the large socially important issues, and a publicly supported extension system to assist in the husbandry and enhancement of small resources is usually held to be desirable.

If the edges of the two-dimensional decision-makers' context can be characterized rather simply, what about those systems lying away from the edges? Some appropriately balanced compromise may be involved. But there appears to be another categorization that meaningfully subdivides the same mean-variance space, that considers the resolution employed in treating problems in the different regions of their space, and that is relevant to decision-makers' needs.

This additional categorization is the distinction between different hierarchical levels of understanding of natural and cultural processes, whereby any particular problem can be attacked at different levels of organization. Virtually all ecological problems, for example, may be usefully investigated at organizational levels ranging from physiological adaptations of particular organs or organ systems to the behaviour of the ecosystem or systems in which that particular problem is embedded. Similar hierarchies can be elaborated in economics, sociology and political practice. Indeed any particular resource problem can involve the considerations of workers from all of these fields at many levels of organization within them. We contend that for any particular problem there is a most relevant level of organization at which to address the problem at least until sufficient understanding has been retained to extend the work upward and downward. Further, it appears essential that interdisciplinary problem-solving activities must, for rapid progress, be directed at matching levels of organization across the participating disciplines.

Returning to a fisheries context and Figure 4.4, we have identified among the listed workers, and their associated problems and fisheries, four levels of organization which characterize their position in the mean-variance diagram: population statics, population dynamics, community statics and community dynamics.

Resource systems dominated by single large unit resources of relatively low variability, have on occasion been modelled to a useful extent by concentrating on the large dominant stocks. The populations thus studied were not very responsive to the stresses of the harvesting process, and where the latter was largely restricted to the stock under study there the impact on the overall community was small. Ecologically such a relatively unresponsive system approximates a static system, at least when equilibrium is achieved, and thus this overall approach has here been labelled "population statics".

The term "population dynamics" is here used to denote systems in which strong interactions occur between populations and the interactions largely vitiate any attempts to model a single stock as though it were dominant or isolated.

Approaching a problem at the level of interacting species, using population dynamics, appears to permit profitable research of systems of higher uncertainty and of greater resource complexity than is the case with population statics. Thus if population statics is largely limited to the lower right subspace of Figure 4.4, population dynamics extends in a somewhat overlapping shell both upward and to the left.

With larger uncertainty, the unit stocks may be characterized by low self-regulatory capabilities or perpetual response and accommodation to fluctuating large exogenous factors. Here these factors may be modelled and the variability of separate resource units related to them. Where resource systems have moderate to great complexity and numerous stocks are of interest, factors exogenous to the actual biological community may in large measure determine the characteristics and productivity of the systems. Again these whole-system variables may be modelled in the first instance. This third shell is here called "community

statics" in that the overall community is not threatened by collapse, displacement or major long-term oscillation as a result of the factors responsible for the uncertainty.

Finally the fourth shell, "community dynamics", involves systems that are seldom in equilibrium, but always responding to or recovering from the ravages of major exogenous factors. Here the whole-system variables that were relatively constant parameters in the third shell, are themselves fluctuating. Those fluctuations need to be understood, initially perhaps in actuarial context by measuring the frequency of major collapse and the approximate length of the period of recovery, and eventually within a dynamic simulation incorporating models of causal mechanisms. The latter model will permit closer tracking of an "optimum" while the former would suffice for purposes of a government-administered insurance mechanism.

As implied in the transdisciplinary approach to the discussion of the four edges of the mean-variance space, there are approaches within the disciplines of ecology, geography, oceanography and limnology, economics, engineering, sociology, political science and managerial science that can be classified according to the four shells shown in Figure 4.4. Those approaches or schools of the various disciplines that fall in the "population statics" shell, for example, should already be broadly congruent conceptually. If so, interdisciplinary research should progress rapidly once semantic differences are overcome. Conversely one should not expect to achieve significant progress quickly by convoking an interdisciplinary team that consisted of an ecologist expert only on a "lower right" kind of system with an economist of the "middle lower", an engineer of the "upper left" and a political scientist of the "middle right".

4.9 Diversity Indices

Use of the word "index" in an ecological context immediately calls to mind a diversity index. This is because diversity has become a popular concept in general ecology and especially in pollution studies. There are many different diversity indices and related measures of evenness, and their numbers are increasing to the point where an initiate to the field is faced with a formidable literature. The following contain partial reviews of the literature: Pielou (1967,1969), Hurlbert (1971), Whittaker (1972), Hill (1973), Heip (1974), Heip and Engles (1974), Peet (1974, 1975), and Clifford and Stephenson (1975).

Species diversity is a function of the number of species (richness) and the distribution of individuals, or other criteria of importance, among the species (evenness or equitability) (Lloyd and Ghelardi, 1964). Several indices have been proposed for each of the two "components" of diversity, while other indices are sensitive to patterns of both richness and evenness. The latter are referred to below as integrated measures.

4.9.1 Richness measures

Hurlbert (1971) has noted that the concept of richness can be divided into "areal species richness" (= species density) which is the number of species collected per unit area, volume, or effort, and "numeric species richness" which is the number of species collected per unit number of individuals. Estimates of species density are independent of species frequency distribution. Clearly this is not true of numeric species richness which can in fact be considered an evenness index.

Species density is the most basic concept of diversity. Obviously it is not an estimate of the total number of species in an assemblage and it is valid only for comparative study. Constant sampling effort can usually be incorporated into survey designs, and the number of species in each collection can be directly compared. If effort varies, Hurlbert's (1971) equation can be used to estimate the number of species that would have been present if effort had been constant (S_{CE}):

$$S_{CE} = \sum_{i=1}^{S_0} \log^{-1} \{[\log(N_0 - n_i)! - \log(N_0 - n_i - N_{CE})!] - [\log N_0! - \log(N_0 - N_{CE})!]\} \quad . . . [1]$$

$$N_{CE} = N_0(E_{CE}/E_0)$$

where: S_{CE} and N_{CE} are the number of species and individuals, respectively, for constant effort.

S_0 and N_0 are the number of species and individuals, respectively, in the original sample.

n_i is the number of individuals of the i^{th} species.

E_{CE} and E_0 are the constant and original sampling efforts.

For all samples, $E_{CE} \leq E_0$.

Estimates of numeric species richness must "adjust" for the dependence of the number of species (S) on the number of individuals (N) collected, i.e. as N increases with further sampling effort, S is likely to increase. One method of adjustment is to plot S against N and consider the resultant curve. This is the basis of Sanders' (1968) rarefaction method. Rarefaction can be accomplished most precisely by the use of equation [1], where $S_{CE} - N_{CE}$ coordinates would be an interpolated point on the curve rather than on an estimate of richness at constant effort. Instead of generating curves, equation [1] could also be used to estimate the number of species at a common N for all collections to be compared. The smallest N for any collection could be selected as this common N. However, relative numeric richness between collections is dependent on the magnitude of the common N. Graphical comparisons are thus preferable. A final caution about using equation [1] in areal or numeric richness comparisons: it assumes that individuals of all species are randomly distributed. If they are aggregated, equation [1] will overestimate S at reduced N (Fager 1972).

A second method for adjusting for the dependence of S on N is to assume a constant relationship between the two: $(S-1)/\ln N$ (Gleason 1922, Margalef 1960); $S/\log N$, $\log S/\log N$, and S/N (Menhinick 1964); $S = \alpha \ln[(N/\alpha) + 1]$, where α = diversity index (Fisher, Corbet and Williams 1943); and the standard deviation (σ') from the log N/S curve, $\log N - \frac{1}{2}(\sigma')^2$ (Edden 1971). Unless observed distributions closely fit one of these theoretical models, it is best to use the rarefaction curves to compare numeric richness.

4.9.2 Evenness and integrated measures

The degree to which an assemblage is dominated by the more abundant species is an important characteristic of the species frequency distribution. Several indices are based upon the probability that a second individual drawn from a collection will belong to the same species as the first:

Simpson's (1949) Index: $$1 - \frac{\sum_{i=1}^{S} n_i (n_i - 1)}{N(N-1)}$$

Hurlbert's (1971) Index: $$1 - \frac{N[1 - \sum_{i=1}^{S} (\frac{n_i}{N})^2]}{N - 1}$$

These indices of "dominance" are not sensitive to the presence of rare species and are independent of sample size.

The Shannon and Brillouin equations, derived from information theory, are integrated measures of diversity:

Shannon: $H' = N \log N - \sum_{i=1}^{S} n_i \log n_i$

Brillouin: $H = \log N! - \sum_{i=1}^{S} \log n_i!$

These have a different theoretical basis. When the removal of a sample has a negligible effect on the total population the Shannon equation is appropriate, but the Brillouin equation should be used when the removed or observed sample is the total population. Shannon's equation has been more widely used for several reasons - it is better known and more easily computed, and can be used when values are other than whole numbers. Neither index is appropriate when there are values of $n_i<1$; this gives negative logs. Despite the fact that the choice of H' or H may be mathematically incorrect, the diversity patterns indicated by both are virtually identical (Boesch 1971, Rex 1973).

The value of H and H' is dependent upon (1) the number of species present, (2) their relative proportions, (3) sample size (N), and (4) the logarithm base - three are used 2, e, and 10. In the above formulation the diversity per sample is given, and this can be standardized by dividing by N to give diversity per individual in a sample. Marked dominance by one species gives low diversity while codominance of several species gives high diversity.

Several evenness indices are based on the ratio of observed diversity to that of a completely equal species frequency distribution. Sometimes a comparative term in the function is drawn from some other model:

Pielou (1969): $J' = H'/H'_{max} = H'/\log S$

Lloyd and Ghelardi (1964): $\epsilon = \frac{S'}{S}$

where S' = number of species predicted by MacArthur's broken stick model.

Hill (1973): $E = \frac{e^{H'}}{S}$

Peet (1975) demonstrated the high sensitivity of evenness indices to slight sample variations and concluded that they are inappropriate for most ecological investigations.

4.9.3 Pollution studies

Though diversity calculations are a part of community analysis, they should neither be the sole nor most important criterion of structure. They may appeal to non-biologists faced with the task of making regulatory decisions and are sometimes presented as the sole criterion of the "health" of marine ecosystems. The trend toward increased reliance on these indices should be reversed for the following reasons:

(1) Diversity indices are not sensitive to spatial-temporal variations in species composition. Assemblages with no species in common can have equal diversities.

(2) There is no clear relationship between diversity patterns and environmental alteration. Human and natural perturbations may increase, decrease, or not affect diversity. Stephenson (personal communication) has shown that standardized Shannon

diversities were unchanged in a benthic assemblage subjected to catastrophic freshwater flooding. Also, fish species diversity often increases in the vicinity of ocean outfalls and thermal discharges (Turner, Ebert, Given 1966, Grimes and Mountain 1971). Because of this uncertainty a diversity index value cannot be established as an environmental quality standard such as those used for chemical parameters.

(3) There is a diversity of diversity indices, none of which can be identified as the "best" index. Our prejudices lead us to favour species density (adjusted for varying effort if necessary), Simpson's (1949) index of dominance, and the Shannon equation. These are measures of different aspects of the very broad concept of diversity. To avoid semantic confusion, they should be referred to as such, not as diversity indices.

Diversity has proven useful in pollution research as a descriptive indication of biological conditions, however, the indices should be employed as an important part of a more comprehensive pollution analysis along with other community, population, and physiological criteria of stress.

5. BIBLIOGRAPHY

ACMRR, Report of the Seventh Session, Advisory Committee on Marine Resources Research, 1974 Rome, 17–24 October 1973. FAO Fish.Rep., (142):45 p.

Alabaster, J.S. et al., An approach to the problem of pollution and fisheries. Symp.Zool. 1972 Soc.Lond., 29:87–114

Angel, M.V. and M.J.R. Fasham, SOND cruise, 1965: factor and cluster analyses of the 1973 plankton results, a general summary. J.Mar.Biol.Assoc.U.K., 53:185–231

__________ SOND cruise, 1965: further factor analyses of the plankton data. J.Mar. 1974 Biol.Assoc.U.K., 54:879–94

Austin, M.P. and I. Noy-Meir, The problem of nonlinearity in ordination: experiments with 1971 two-gradient models. J.Ecol., 59:763–73

Bachman, R.W. and J.R. Jones, Phosphorus inputs and algal blooms in lakes. Iowa State J. 1974 Res., 49:155–60

Baker, J.M., Recovery of salt marsh vegetation from successive oil spillages. Environ. 1973 Pollut., 4:223–30

Ball, I.R., The relative susceptibilities of some species of freshwater fish to poisons. 1967 2. Zinc. Water Res., 1:773–83

Balon, E.K., Fish production of a tropical ecosystem. In Lake Kariba: a man-made 1974 tropical ecosystem in Central Africa, edited by E.K. Balon and A.G. Coche, The Hague, Dr. W. Junk C.V. Publ., pp. 249–616

__________ Reproductive guilds of fishes: a proposal and definition. J.Fish.Res. 1975 Board Can., 32:821–64

__________, Ecological guilds of fishes: a short summary of the concept and its 1975a application. Verh.Int.Ver.Theor.Angew.Limnol., (in press)

Barbour, C.D. and J.H. Broom, Fish species diversity in lakes. Am.Nat., 108:473–89 1974

Beals, E.W., Ordination: Mathematical elegance and ecological naïveté. J.Ecol., 1973 61:23–35

Bella, D.A., Fundamentals of comprehensive environmental planning. Engineering issues, 1974 J.Prof.Activities Proc.Am.Soc.Civil Eng., 100(EI1):17–36

Bella, D.A. and W.S. Overton, Environmental planning and ecological possibilities. 1972 J.Sanit.Eng.Div.Am.Civil Eng., 98(SA3):579–92

Beverton, R.J.H., Comment. In The Way Ahead. Symposium of the Fisheries Research Board 1974 of Canada. General Discussion. J.Fish.Res.Board Can., 31(7):1308

Beverton, R. and S. Holt, On the dynamics of exploited fish populations. Fish.Invest., 1957 Lond.(2), (19):533 p.

Bishop, J.E., Limnology of a small Malayan River, Sungai Gombak. The Hague, Dr. W. Junk 1973 B.V., 485 p.

Boesch, D.F., Distribution and structure of benthic communities in a gradient estuary. 1971 Ph.D. Thesis, College of William and Mary, Williamsburg, Virginia, 120 p.

Boney, A.D., Toxicity studies with an oil-spill emulsifier and the green algae
1970 Prasinocladus marinus. J.Mar.Biol.Assoc.U.K., 50:461-73

Box, G. and G. Jenkins, Time series analysis: forecasting and control. San Francisco,
1970 Holden-Day

Brillouin, L., Science and information theory. New York, Academic Press
1962

Bryson, R.A., Drought in Sahelia: who or what is to blame. Ecologist, 3(10):366-71
1973

Buchanan, J.B., Dispersal and demography of some infaunal echinoderm populations. Symp.
1967 Zool.Soc.Lond., 20:1-11

Bush, R.M., E.B. Welch and B.W. Mar, Potential effects of thermal discharges in aquatic
1974 systems. Environ.Sci.Technol., 8:561-8

Caddy, J., Long-term trends and evidence for production cycles in the Bay of Fundy scallop
1974 fishery. Paper presented to the ICES 62nd Statutory Meeting. Shellfish and benthos committee (K:40):1 p.

Cairns, J., Jr. and K.L. Dickson, A simple method for the biological assessment of the
1971 effects of waste discharges on aquatic bottom-dwelling organisms. J.Water Pollut.Control Fed., 43:755-72

Cairns, J., Jr. et al., The sequential comparison index - a simplified method for non-
1968 biologists to estimate relative differences in biological diversity in stream pollution studies. J.Water Pollut.Control Fed., 40:1607-13

__________, The recovery of damaged streams. Biol.Bull.Assoc.Southeast., 18(3):79-106
1971

Cassie, R.M. and A.D. Michael, Fauna and sediments of intertidal mud flat: a multivariate
1968 analysis. J.Exp.Mar.Biol.Ecol., 2(1):1-23

Christie, W.J. and H.A. Regier, Temperature as a major factor influencing reproductive
1973 success of fish - two examples. Rapp.Procès-Verbaux Cons.Int.Explor.Mer., 164:208-18

Clifford, H.T. and W. Stephenson, An introduction to numerical classification. New York,
1975 Academic Press, 229 p.

Connell, J.H., A predator-prey system in the marine intertidal region. Ecol.Monogr.,
1970 40(1):49-78

Connor, P.M., Acute toxicity of heavy metals to some marine larvae. Mar.Pollut.Bull.,
1972 3:190-2

Coutant, C.C., Thermal pollution - biological effects. J.Water Pollut.Control Fed.,
1971 43:1292-334

Cowell, E.B., The effects of oil pollution on salt-marsh communities in Pembrokeshire
1969 and Cornwall. J.Appl.Ecol., 6:133-42

__________, Oil pollution in perspective. In The ecological effects of oil pollution on
1971 littoral communities, edited by E.B. Cowell, London. Institute of Petroleum, pp. 224-39

Cowell, E.B., A critical examination of present practice. In Ecological aspects of toxicity
1974 testing of oils and dispersants, edited by L.R. Beynon and E.B. Cowell, London, Applied Science Publ., pp. 97-104

Cowell, E.B. and J.M. Baker, Recovery of a salt marsh in Pembrokeshire, South-West Wales,
1969 from pollution by crude oil. Biol.Conserv., 1:291-5

Cowell, E.B. and J.H. Crothers, On the occurrence of multiple rows of 'teeth' in the shell
1970 of the dog-whelk Nucella lapillus. J.Mar.Biol.Assoc.U.K., 50:1101-11

Crisp, D.J. (Ed.), The effects of the severe winter of 1962-63 on marine life in Britain.
1964 J.Anim.Ecol., 33:165-210

Cuinat, R. et al., Ecological diagnosis in salmonid streams. European Inland Fisheries
1970 Advisory Commission. Rome, FAO, EIFAC 70/SC I-1:71 p.

Cuinat, R., Diagnoses écologiques dans quatre rivières à truites de Normandie. Ann.
1971 Hydrobiol., 2:69-134

Curlin, J.W., Environmental Indices. Environmental Policy Division, Congressional Research
1973 Service, Library of Congress. Washington, D.C., U.S. Government Printing Office, 46 p.

Dahlberg, M.P. and E.P. Odum, Annual cycles of species occurrence, abundance and diversity
1970 in Georgia estuarine populations. Am.Midl.Nat., 83:382-92

Davis, C.C., The effects of pollutants on the reproduction of marine organisms. In Marine
1972 pollution and sea life, edited by M. Ruivo, West Byfleet, Surrey, Fishing News (Books) Ltd., pp. 305-11

Day, J.H., J.G. Field and M.P. Montgomery, The use of numerical methods to determine the
1971 distribution of benthic fauna across the continental shelf off North Carolina. J.Anim.Ecol., 40:93-123

Dayton, P.K., Competition, disturbance and community organisation. Ecol.Monogr.,
1971 41:351-89

Dayton, P.K. et al., Biological accommodation in the benthic community at McMurdo Sound,
1974 Antarctica. Ecol.Monogr., 44(1):105-28

Dill, W.A., D.W. Kelly and J.C. Fraser, The effects of water- and land-use development on
1971 the aquatic environment and its resources and solutions to some of the generated problems. FAO Fish.Circ., (129):7 p.

Dillon, P.J. and F.H. Rigler, The phosphorus-chlorophyll relationship in lakes. Limnol.
1974 Oceanogr., 19:767-73

Dunst, R.C. et al., Survey of lake rehabilitation techniques and experiences. Tech.Bull.
1974 Wisc.Dep.Nat.Resour., (75):79 p.

Edden, A.C., A measure of species diversity related to the lognormal distribution of
1971 individuals among species. J.Exp.Mar.Biol.Ecol., 6:199-209

Eisenbud, M. et al., Planning for environmental indices. U.S. National Academy of Sciences/National Academy of Engineering (MS) (in press)

Fager, E.W., Communities of organisms. In The sea: ideas and observations on progress in
1963 the study of the seas, edited by M.N. Hill. New York, Wiley, pp. 415-33

Fager, E.W., Diversity: a sampling study. Am.Nat., 106:293-310
1972

Fager, E.W. and J. McGowan, Zooplankton species groups in the North Pacific. Science, Wash., D.C., 140:453-60
1963

Field, J.G., A numerical analysis of changes in the soft-bottom fauna along a transect across False Bay, South Africa. J.Exp.Mar.Biol.Ecol., 7:215-53
1971

Fish, H., Fisheries and amenity requirements. Effluent Water Treatment J., Sept. 1973:586-97
1973

Fisher, R.A., A.S. Corbet and C.B. Williams, The relation between the number of species and the number of individuals in a random sample of an animal population. J.Anim. Ecol., 12:42-58
1943

Fonselius, S.H., Hydrography of the Baltic Deep Basins. 3. Rep.Fish.Board Swed.(Hydrogr.), (23)
1969

__________, On the stagnant conditions in the Baltic. Dissertation, Gothenburg
1969a

Frey, D.G., Paleolimnology. Mitt.Int.Ver.Theor.Agnew.Limnol., 20:95-123
1974

Fritts, H. et al., Multivariate techniques for specifying tree growth and climate relationships and for reconstructing anomalies in paleoclimate. J.Appl.Meteorol., 10(5):845-64
1974

Gadgil, M. and O.T. Solbrig, The concept of R and K selection: evidence from wildflowers and some theoretical considerations. Am.Nat., 106:14-31
1972

Gage, J., Shallow-water zonation of sea-lock benthos and its relation to hydrographic and other physical features. J.Mar.Biol.Assoc.U.K., 54:223-49
1974

Galbraith, J.K., Economics and the public purpose. Houghton Mifflin, Boston, 334 pp.
1973

Ganf, G.G. and A.B. Viner, Ecological stability in a shallow equatorial lake (Lake George, Uganda). Proc.R.Soc.Lond.(B), 184:321-46
1973

GFCM, Report of the Second Session of the GFCM Working Party on Marine Pollution in Relation to the Protection of Living Resources, Monte Carlo, 16-18 September, 1974. Rome, FAO, General Fisheries Council for the Mediterranean, GFCM/POLL/74.2:18 p.
1974

Gleason, H.A., On the relation between species and area. Ecology, Durham, N.C., 3:158-62
1922

Goodman, G. et al., North Atlantic Treaty Organization Provisional Report of a Working Group on Environmental Indicator Organisms held at the School of Biological Sciences, University of Sussex, U.K., 1-5 April 1974 (mimeo)
1974

Gower, J.C., Some distance properties of latest root and vector methods used in multivariate analysis. Biometrika, 53:325-38
1966

__________, Multivariate analysis and multidimensional geometry. Statistician, 17:13-28
1967

Gray, J.S., Animal-sediments relationships. Oceanogr.Mar.Biol., 12:223-61
1974

Greeson, P.E., Stream classification of the Dix River, Kentucky, shown by fish distribution
1963 and water analysis. M.S. Thesis, University of Kentucky, Lexington, 49 p.

Grimes, C.B. and J.A. Mountain, Effects of thermal effluent upon marine fishes near the
1971 Crystal River steam electric station. Prof.Pap.Ser.Fla.Dep.Nat.Resour., (17):64 p.

Gross, B.M., The state of the nation: social systems accounting. London, Tavistock Publ.,
1966 166 p.

Hackney, P.A. and C.K. Minns, A computer model of biomass dynamics and food competition
1974 with implications for its use in fishery management. Trans.Am.Fish.Soc., 103:215-25

Hallam, A., The interpretation of size-frequency distributions in molluscan death
1967 assemblages. Paleontology, 10:25-42

Harrel, R.C., B.J. Davis and T.C. Dorris, Stream order and species diversity in fishes in
1967 an intermittent Oklahoma stream. Am.Midl.Nat., 78:428-36

Heip, C., A new index measuring evenness. J.Mar.Biol.Assoc.U.K., 54:555-7
1974

Heip, C. and P. Engles, Comparing species diversity and evenness indices. J.Mar.Biol.
1974 Assoc.U.K., 54:559-63

Hellawell, J., Biological surveillance and water quality monitoring. Rome, FAO,
1974 EIFAC/74/III-1:16 p.

Hempel, G. and W. Nellen, Fische der Ostsee. In Meereskunde der Ostsee, edited by
1974 L. Magaard and G. Rheinheimer. Berlin, Springer-Verlag

Henderson, H.F., Programa de evaluación de recursos para apoyar el desarrollo pesquero en
1974 las aguas continentales de México. Programa de Investigaciones y Fomento Pesqueros México/PNUD/FAO. Contrib.Estud.Pesq.Méx., (CEPM.8):62 p.

Henderson, H.F. and R.L. Welcomme, The relationship of yield to morpho-edaphic index and
1974 numbers of fishermen in African inland fisheries. Rome, FAO, CIFA/OP 1:19 p.

Henderson, H.F., R.A. Ryder and A.W. Kudhongania, Assessing fishery potentials of lakes
1973 and reservoirs. J.Fish.Res.Board Can., 30(12)Pt.2:2000-9

Hildebrand, H.H. and G. Gunter, Correlations of rainfall with the Texas catch of white
1953 shrimp, Penaeus setiferus (Linnaeus). Trans.Am.Fish.Soc., 82:151-5

Hill, M.O., Diversity and evenness: a unifying notation and its consequences. Ecology,
1973 Durham, N.C., 54:427-32

Hocutt, C.H. et al., Biological assessment of water quality in a large river system: an
1974 evaluation of a method for fishes. Rome, FAO, EIFAC/74/1/Symp.55:20 p.

Holling, C.S., Resilience and stability of ecological systems. Ann.Rev.Ecol.System.,
1973 4:1-23

Hrbáček, J., Relations between some environmental parameters and the fish yield as a basis
1969 for a predictive model. Verh.Int.Ver.Theol.Angew.Limnol., 17:1069-81

_______, Relations of productivity phenomena to the water quality criteria in ponds
1969a and reservoirs. Adv.Water Pollut.Res., 4:717-24

Huet, M., The evaluation of the fish productivity in fresh waters (the coefficient of
1964 productivity k). Verh.Int.Ver.Theor.Agnew.Limnol., 15:524-8

Hughes, R.N. and M.L.H. Thomas, The classification and ordination of shallow water benthic
1971 samples from Prince Edward Island, Canada. J.Exp.Mar.Biol.Ecol., 7:1-39

__________, Classification and ordination of benthic samples from Bedeque Bay, an
1971a estuary of Prince Edward Island, Canada. Mar.Biol., 10:227-35

Hurlbert, S.H., The nonconcept of species diversity: a critique and alternate parameters.
1971 Ecology, Durham, N.C., 52:577-86

Inhaber, H., Environmental quality: outline for a national index for Canada. Science,
1974 Wash.D.C., 186:798-805

Isaacs, J.D., Unstructured marine food webs and "pollutant analogues". Fish.Bull.NOAA/NMFS,
1972 70:1053-9

Jantsch, E., Technological planning and social futures. London, Cassell/Associated Business
1972 Programmes, 265 p.

Jenkins, R.M., The influence of some environmental factors on standing crops of fishes in
1967 U.S. reservoirs. In Proceedings of the Reservoir Fishery Resources Symposium, Southern Division, American Fisheries Society, pp. 298-321

Jenkins, G. and D. Watts, Spectral analysis and its application. San Francisco, Holden-Day,
1968 XVIII, 525 p.

Katz, L.M., The effects of water soluble fraction of crude oil on larvae of Decapod
1973 Crustacea. Environ.Pollut., 5:199-204

Kerr, S.R., Structural Analysis of aquatic communities. In Proceedings of the First
1974 International Congress on Ecology, The Hague. Wageningen, The Netherlands Centre for Agricultural Publishing and Documentation

Knight, W. and A.V. Tyler, Are species association coefficients really necessary? Tech.
1973 Rep.Fish.Res.Board Can., (397):8 p.

__________ A method for compression of species association data by using habitat
1973a preferences, including an analysis of fish assemblages on the southwest Scotian Shelf. Tech.Rep.Fish.Res.Board Can., (402):15 p.

Korringa, P., Water temperature and breeding throughout the geographical range of
1957 Ostrea edulis. Ann.Biol.CIEM, 33:1-17

Krenkel, P.A. and F.L. Parker, Biological aspects of thermal pollution. Nashville, Tenn.,
1969 Vanderbilt University Press, 407 p.

Kuehne, R.A., Differences in coefficients of similarity for invertebrates in adjacent
1967 normal and polluted streams. Bull.Ecol.Soc.Am., 48:57-8

__________, Applications of the Horton stream classification to evaluate faunal studies.
1970 Proc.Ser.Am.Water Resour.Assoc., (8):367-70

Larkin, P.A., Freshwater pollution, Canadian style. Montreal, McGill-Queen's University
1974 Press, 132 p.

Leighton, D.L., L.G. Jones and W.J. North, Ecological relationships between giant kelps
1966 and sea urchins in Southern California. Proc.Int.Seaweed Symp., 5:141-53

Lett, P., Untitled comments in discussion following Balon (1975a)
1975

Levin, A.R. et al., Thermal discharges: ecological effects. Environ.Sci.Technol.,
1972 6:224-30

Lewis, J.R., The ecology of rocky shores. London, EUP, 323 p.
1964

__________, Problems and approaches to base-line studies in coastal communities.
1970 In Marine pollution and sea life, edited by M. Ruivo. West Byfleet, Surrey, Fishing News (Books) Ltd., pp. 401-4

Lewis, J.R. and R.S. Bowman, Local habitat-induced variations in the population dynamics
1975 of Patella vulgata L. J.Exp.Mar.Biol.Ecol., 17:165-203

Lie, V. and J.C. Kelley, Benthic infauna communities off the coast of Washington and in
1970 Puget Sound: identification and distribution of the communities. J.Fish.Res. Board Can., 27:621-51

Lindquist, A., Effects of marine pollution on populations and community structure.
1972 Rome, FAO, FIR/TPLR/72/25:15 p.

Lloyd, M. and R.J. Ghelardi, A table for calculating the equitability component of species
1964 diversity. J.Anim.Ecol., 33:217-25

Lotrich, V.A., Growth, production and community composition of fishes inhabiting a 1st,
1969 2nd and 3rd order stream of eastern Kentucky. Ph.D. Thesis, University of Kentucky, Lexington, 97 p.

Loubens, G., Etude de certains peuplements ichtyologiques par des pêches au poison. 1re note
1969 Cah.ORSTOM (Hydrobiol.), 3(2):45-73

__________, Etude de certains peuplements ichtyologiques par des pêches au poison.
1970 2e note. Cah.ORSTOM (Hydrobiol.), 4(1):45-61

MacFadyen, A., Some thoughts on the behaviour of ecologists. J.Ecol., 63(2):379-91
1975

Mar, B.W. et al., Analysis of engineering alternatives for environmental protection from
1973 thermal discharges. Environ.Protect.Technol.Ser., Wash.D.C., (73-161):235 p.

Margalef, R., Temporal succession and spatial heterogeneity in phytoplankton. In
1960 Perspectives in marine biology, edited by A.A. Buzzati-Traverso. Berkeley, Calif., University of California Press

McErlean, A.J. and J.A. Mihursky, Species diversity - species abundance of fish populations:
1969 an examination of various methods. Proc.Annu.Conf.Southeast.Assoc.Game Fish.Comm. 22:367-72

McErlean, A.J. et al., Abundance, diversity, and seasonal patterns of estuarine fish
1973 populations. Estuar.Coast.Mar.Sci., 1:19-36

Menhinick, E.F., A comparison of some species - individuals diversity indices applied to
1964 samples of field insects. Ecology, Durham, N.C., 45:859-61

Mileikovsky, S., On predation of pelagic larvae and early juveniles of marine bottom
1974 invertebrates by adult benthic invertebrates and their passing alive through their predators. Mar.Biol., 26:303-11

Mironov, O.G., The effect of oil pollution on the flora and fauna of the Black Sea. In
1972 Marine pollution and sea life, edited by Mr. Ruivo. West Byfleet, Surrey, Fishing News (Books) Ltd., pp. 222-4

Moore, P.G., The kelp fauna of northeast Britain. 3. Qualitative and quantitative
1974 ordinations, and the utility of a multivariate approach. J.Exp.Mar.Biol.Ecol., 16:257-300

Nash, C.B., Associations between fish species in tributaries and shore waters of western
1950 Lake Erie. Ecology, Durham, N.C., 31:561-6

National Academy of Sciences and National Academy of Engineering, Planning Committee on
1974 Environmental Indices 1974 (Final Report, Oct. 31, 1974). Planning for environmental indices. Report to the Environmental Studies Board of the Commission on Natural Resources of the National Research Council. Washington, D.C., National Academy of Sciences and National Academy of Engineering, 47 p.

Nelson, C., Applied time series for managerial forecasting. San Francisco, Holden-Day
1973

Newell, W.T. and J. Newton, Computer simulation game models for ecology and natural
1968 resources management. Pap.Cent.Quantit.Sci.Univ.Wash., (2):30 p.

Odum, E.P., The strategy of ecosystems development. Science, Wash.D.C., 164:262-70
1969

Paine, R.T., Food web complexity and species diversity. Am.Nat., 100:65-75
1966

______, A note on trophic complexity and community stability. Am.Nat., 103:91-3
1969

______, Intertidal community structure. Experimental studies on the relationship
1974 between a dominant competitor and its principle predator. Oecologia, 15:93-120

Pattee, H.H., The problem of biological hierarchy. In Towards a theoretical biology,
1970 edited by C.H. Waddington. Chicago, Aldine Publ. Co.

Peet, R.K., The measurement of species diversity. Ann.Rev.Ecol.System., 5:285-307
1974

______, Relative diversity indices. Ecology, Durham, N.C., 56:496-8
1975

Petersen, C.G.J., Valuation of the sea. 2. The animal communities of the sea bottom and
1914 their importance for marine zoogeography. Rep.Dan.Biol.Stn., 21:1-44

Pielou, E.C., The use of information theory in the study of the diversity of biological
1967 populations. Proc.Berkeley Symp.Math.Statist.Probab., 5, Vol.4:163-77

______, An introduction to mathematical ecology. New York, Wiley-Interscience, 286 p.
1969

Quayle, D.B., Distribution of introduced marine mollusca in British Columbia waters.
1964 J.Fish.Res.Board Can., 21:1155-81

Rao, C., Linear statistical inference and its applications. New York, John Wiley & Sons,
1973 Inc., 625 p.

Regier, H.A., Sequence of exploitation of stocks in multispecies fisheries in the Laurentian
1973 Great Lakes. J.Fish.Res.Board Can., 30:1992-9

_______, Fishery ecology: A perspective for the near future. J.Fish.Res.Board Can.,
1974 31(7):1303-6

_______, To survey, monitor or appraise fishery resources: some general concepts.
1975 EIFAC Tech.Pap., (23) Suppl.1 Vol.2:690-703

Regier, H.A. and E.B. Cowell, Applications of ecosystem theory: succession, diversity,
1972 stability, stress and conservation. Biol.Conserv., 5:83-8

Regier, H.A. and H.F. Henderson, Towards a broad ecological model of fish communities and
1973 fisheries. Trans.Am.Fish.Soc., 102:56-72

Regier, H.A. and K.H. Loftus, Effects of fisheries exploitation on salmonid communities
1972 in oligotrophic lakes. J.Fish.Res.Board Can., 29:959-68

Regier, H.A., P.L. Bishop and D.J. Rapport, Planned transdisciplinary approaches:
1974 renewable resources and the natural environment, particularly fisheries.
J.Fish.Res.Board Can., 31:1683-703

Rex, M.A., Deep-sea species diversity: decreased gastropod diversity at abyssal depths.
1973 Science, Wash., D.C., 181:1051-3

Rosenburg, R., Benthic faunal recovery in a Swedish fjord following the closure of a
1972 sulphite pulp mill. Oikos, 23:92-108

Ryder, R.A., A method for estimating the potential fish production of north-temperate
1965 lakes. Trans.Am.Fish.Soc., 94:214-8

Ryder, R.A. et al., The morphoedaphic index, a fish yield estimator - review and
1974 evaluation. J.Fish.Res.Board Can., 31:663-88

Sanders, H.L., Marine benthic diversity: a comparative study. Am.Nat., 102:243-82
1968

Sastry, A.N., Temperature effects in reproduction of bay scallop Aequipecten irradians L.
1966 Biol.Bull.Mar.Biol.Lab., Woods Hole, 130:118-34

Schindler, D.W., Experimental approaches to limnology - an overview. J.Fish.Res.Board Can.,
1973 30(10):1409-13

Selye, H., Stress without distress. Philadelphia, J.B. Lippincott Co., 171 p.
1974

Shannon, C.E., A mathematical theory of communication. Urbana, University of Illinois Press
1948

Sheldon, R., Fossil communities with multi-model size-frequency distributions. Nature, Lond.
1965 206:1336-8

Silver, M.W., The habitat of Salpa fusiformis in the California Current as defined by
1975 indicator assemblages. Limnol.Oceanogr., 20:230-7

Simpson, E.H., Measurement of diversity. Nature, Lond., 163:688 p.
1949

Sjöberg, S., F. Wulff and P. Wåhlström, The use of computer simulations for systems
1972 ecological studies in the Baltic. Ambio, 1(6):217-22

Sládeček, V., System of water quality from the biological point of view. Arch.Hydrobiol.,
1973 Beih., 7:1-218

__________, The reality of three British biotic indices. Water Res., 7:995-1002
1973a

Sneath, P.H.A. and R.R. Sokal, Numerical taxmonomy: the principles and practice of
1973 numerical classification. San Francisco, Freeman, 573 p.

Southward, A.J., The population balance between limpets and seaweeds on wave-beaten rocky
1956 shores. Rep.Mar.Biol.Stn., Port Erin, (68):21-9

Southward, A.J., E.I. Butler and L. Pennycuik, Recent cyclic changes in climate and in
1975 abundance of marine life. Nature, Lond., 253:714-9

Southward, G. and D. Chapman, Utilization of Pacific halibut stocks: study of Bertalanffy's
1965 growth equation. Rep.IPHC, (39)

Stephen, A.C., Production of large broods in certain marine lamellibranchs with a
1938 possible relation to weather conditions. J.Anim.Ecol., 7:130-43

Stephenson, W., The use of computers in classifying marine bottom communities. In
1973 Oceanography of the South Pacific, 1972, compiled by R. Fraser. Wellington, New Zealand National Committee for Unesco, pp 463-73

__________, The validity of the community concept in marine biology. Proc.R.Soc.Queensl.,
1973a 84:73-86

Stephenson, W. and W.T. Williams, A study of the benthos of soft bottoms, Sek Harbour,
1971 New Guinea, using numerical analysis. Aust.J.Mar.Freshwat.Res., 22:11-34

Stephenson, W., S.D. Cook and Y.I. Raphael, The effect of a major flood on the macrobenthos of Bramble Bay, Moreton Bay. Mem.Queensl.Mus. (MS)

Stephenson, W., Y.I. Raphael and S.D. Cook, The macrobenthos of Bramble Bay, Moreton Bay.
1976 Mem.Queensl.Mus., 18 (in press)

Stephenson, W., W.T. Williams and S. Cook, Computer analyses of Petersen's original data
1972 on bottom communities. Ecol.Monogr., 42:387-415

__________, The macrobenthos of soft bottoms in southern Moreton Bay. Mem.Queensl.Mus.,
1974 17:73-124

Straškraba, M., Limnological basis for modelling reservoir ecosystems. Geophys.Monogr.,
1973 17:517-38

__________, Development of an analytical phytoplankton model with parameters empirically
1974 related to dominant controlling variables. Abh.Dtsch.Akad.Wiss., (in press)

Sutcliffe, W.H., Jr., Correlations between seasonal river discharge and local landings of
1973 American lobster (Homarus americanus) and the Atlantic halibut (Hippoglossus hippoglossus) in the Gulf of St. Lawrence. J.Fish.Res.Board Can., 30:856-9

Sutherland, J.P., Multiple stable points in natural communities. Am.Nat., 108(964):859-73
1974

_____, Alternate steady-states. Am.Nat. (in press)

Swingle, H.S. and W.E. Swingle, Problems in dynamics of fish populations in reservoirs.
1967 In Proceedings of the Reservoir Fishery Resources Symposium, Southern Division, American Fisheries Society, pp. 229-43

Taylor, L.R., Aggregation, variance and mean. Nature, Lond., 189:732-5
1961

_____, Aggregation as a species characteristic for statistical ecology. In
1971 Statistical ecology: proceedings of the international symposium, edited by G.P. Patel, E.C. Pielou and W.E. Waters. Philadelphia, Pennsylvania State University Press, University Park, Vol.1:356-77

Thom, R., Topological models in biology. In Towards a theoretical biology, edited by
1970 C.H. Waddington, Chicago, Aldine Publ. Co., Vol. 3

Thomas, W.A. (Ed.), Indicators of environmental quality. New York, Plenum Press, 275 p.
1972

Thomas, W.A., G. Goldstein and W.H. Wilcox, Biological indicators of environmental quality:
1973 a bibliography of abstracts. Ann Arbor, Ann Arbor Scientific Publishers Inc., 254 p.

Thorson, G., Some factors influencing the recruitment and establishment of marine benthic
1966 communities. Neth.J.Sea Res., 3:267-93

Thurow, F., Fischerei. In Meereskunde der Ostsee, edited by L. Magaard and G. Rheinheimer.
1974 Berlin, Springer-Verlag

Tsai, Chu-Fa, Effects of sewage treatment plant effluents on fish: a literature review.
1975 Contrib.Univ.Md.Cent.Environ.Estuar.Stud., (637):229 p.

Turner, C.H., E.E. Ebert and R.R. Given, The marine environment in the vicinity of the
1966 Orange County Sanitation District's ocean outfall. Calif.Fish.Game, 52:28-48

Tyler, A.V., Periodic and resident components in communities of Atlantic fishes. J.Fish.
1971 Res.Board Can., 28:935-46

_____, Food resource division among northern, marine, demersal fishes. J.Fish.Res.
1972 Board Can., 29:997-1003

_____, Community analyses. In Benthos of lakes, edited by R.O. Brinkhurst.
1974 London, Macmillan, pp. 65-83

_____, User's manual for PISCES: a general fish population simulator and fisheries
1974a game program. Tech.Rep.Fish.Mar.Ser.Environ.Can., (480):30 p.

U.S. Government Executive Office of the President, Office of Management and Budget, Social
1973 indicators, 1973. Washington, D.C., U.S. Government Printing Office, 258 p.

Verduin, J., Reservoir management problems created by increased phosphorus levels of
1967 surface waters. In Proceedings of the Reservoir Fishery Resources Symposium, Southern Division, American Fisheries Society, pp. 200-6

Walters, C., An interdisciplinary approach to development of watershed simulation models.
1975 J.Fish.Res.Board Can., 32:177-95

Watt, K.E.F., The Titanic effect. Stamford, Conn., Sinauer Assoc., Publ., 268 p.
1974

Webb, T. and R. Bryson, Late- and postglacial climatic change in the northern Midwest, U.S.A.:
1972 quantitative estimates derived from fossil pollen spectra by multivariate statistical analysis. Quaternary Res., 2:70-115

Welcomme, R.L., Some general and theoretical considerations on the fish production of
1974 African rivers. CIFA Occas.Pap., (3):26 p.

__________, The fisheries ecology of African floodplains. CIFA Tech.Pap., (3):51 p.
1975

Whittaker, R.H., Evolution and measurement of species diversity. Taxon, 21:213-51
1972

Williams, W.T. and W. Stephenson, The analysis of three-dimensional data (sites x
1973 species x times) in marine ecology. J.Exp.Mar.Biol.Ecol., 11:207-27

Whurmann, K., Some problems and perspectives in applied limnology. Mitt.Int.Ver.Theor.
1974 Agnew.Limnol., 20:324-402

Wulff, F., Ecological data and the model. Proceedings of the Second Soviet-Swedish
1976 Symposium on the Control of the Baltic Sea Pollution, Riga, September 1973. (To be published in Ambio, Special Report, Spring 1976)

Anon., Fish and water-quality criteria. Notes Water Pollut.Water Res.Cent.U.K., (65):
1974 4 p.

[J. Wildlife Management, 1954. Vol.18(1) is an issue devoted entirely to cyclic population behaviour.]

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